BAYESIAN INFERENCE OF FISHERIES AND ECOLOGY MODELS

A DISSERTATION

SUBMITTED TO THE GRADUATE SCHOOL

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS

FOR THE DEGREE

DOCTORATE OF PHILOSOPHY

BY

JASON C. DOLL

DISSERTATION ADVISOR: DR. THOMAS E. LAUER

BALL STATE UNIVERSITY

MUNCIE, INDIANA

DECEMBER 2015

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BALL STATE UNIVERSITY
MUNCIE, INDIANA
DECEMBER 2015

ABSTRACT

DISSERATION: Bayesian Inference of Fisheries and Ecology Models

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The goal of fisheries and ecology research is to understand the dynamics of the natural world. To achieve this goal two statistical paradigms are used, frequentist and Bayesian inference. While frequentist inference remains the dominant statistical method in fisheries and ecology, there are many advantages to a Bayesian approach. The goal of this dissertation is to evaluate fisheries and ecology models using Bayesian inference to answer key environmental problems. My specific objectives are; 1) evaluate covariates of Walleye *Sander vitreus* recruitment to age-0 from stocked populations in six Midwestern Reservoirs; 2) evaluate yield-per-recruit models of Walleye and hybrid striped bass in a Midwestern Reservoir; 3) estimate electrofishing capture probabilities while accounting for schooling behavior of common stream fishes. A Bayesian approach allowed me to identify that Walleye recruitment was affected by the number of stocking events, moronid stocking abundance, and maximum discharge. However, the magnitude and direction of the effect varied among reservoirs. I also determined management strategies that can be used to obtain maximum yield of two competing piscivores while accounting for uncertainty in model inputs. Finally, I developed a model that described capture probabilities of stream fish while accounting for schooling behavior. This model was a more accurate method compared to the traditional model.

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Dedication

I dedicate this dissertation to my family, especially to Mom and Dad for their support and instilling in me the importance of hard work.

Chapter 1: Dissertation Background and Objectives

The goal of fisheries and ecology research is to understand the dynamics of the natural world using the scientific method. The scientific method operates by observing a particular phenomenon followed by formulating a hypothesis to explain the observation, constructing an experimental design to evaluate the hypothesis, collect data, and use the data to evaluate the validity of your hypothesis. Two statistical paradigms are used to make a decision about a hypothesis given the observed data, frequentist and Bayesian inference.

Bayesian inference is a statistical inference paradigm that describes probability differently than traditional frequentist inference (Ellison 1996). Frequentist inference treats parameters as fixed unknown values, the data as random, and inference is drawn from 95% confidence intervals that are based on hypothetical replicates. In contrast, Bayesian inference, treats parameters as random, data are considered fixed, and inference is drawn from posterior distributions of a parameter given the data, the model, and the prior belief about the parameter.

Bayesian inference is often considered subjective because it relies on specification of prior distributions. Fortunately, work has been devoted to non-informative priors to reduce or eliminate subjectivity (Berger 2006). For example, non-informative prior distributions result in posterior distributions that are largely due to the likelihood function and thus are generally similar to results of frequentist inference when evaluating simple models (e.g., linear regression). However, the value of prior information should not be discounted and Bayesian inference provides a transparent mechanism for its inclusion (Kuhnert et al. 2010).

Bayesian inference uses probability theory as a formal way of incorporating new data with previous knowledge to make a direct conclusion about a hypothesis. The foundation of Bayesian inference is based on Bayes' theorem where the probability of a model parameter (θ)

given observed data (X) is estimated using the data, the prior belief about θ, and the evidence. According to Bayes' theorem the posterior probability of model parameters given observed data $p(\theta|X)$ is calculated by:

$$\text{Equation 1:} \quad p(\theta|X) = \frac{p(X|\theta)p(\theta)}{\int d\theta \; p(X|\theta)p(\theta)}$$

Here, $p(X|\theta)$ denotes the probability of the data (X) given the parameters (the likelihood function), $p(\theta)$ denotes the prior probability of the model parameters, and the denominator (the evidence) is a normalizing parameter calculated by summing across all possible parameter values weighted by the strength of their belief. For a thorough review of Bayesian inference, see Gelman et al. (2004), Carlin and Louis (2008), and Kruschke (2011).

Frequentist inference remains the dominant statistical method in fisheries and ecology, however, the advantages of Bayesian inference are well documented (Austin 2001; Broomhall et al. 2010; Kruschke 2010; Kruschke 2013; Wagner et al. 2013). For example, using the Bayesian framework spawning stock biomass from fisheries stock assessments decreased using uniform priors (Nielsen and Lewy 2002), phylogenetic accuracy has been increased thus providing a more ecologically realistic model (Alfaro et al. 2003) and informative priors in terms of distributional assumptions can be used to construct a more ecologically realistic model (Doll and Lauer 2014).

The goal of this dissertation is to evaluate fisheries and ecology models to answer key environmental problems using Bayesian inference. This dissertation will address three questions that are often difficult to answer using traditional frequentist methods; 1) What factors determine successful recruitment; 2) What is the predicted harvested yield of a sport fish under variable management scenarios; 3) How does schooling behavior of fish influence sampling gear efficiency? These are three fundamental questions that will have implications to fisheries

managers, ecologists, and modelers. To address these questions our specific objectives include; 1) evaluate covariates of Walleye *Sander vitreus* recruitment to age-0 from stocked populations in six Midwestern Reservoirs; 2) evaluate a Beverton-Holt yield-per-recruit model of Walleye and hybrid striped bass in a Midwestern Reservoir; 3) estimate electrofishing capture probabilities while accounting for schooling behavior of common stream fish.

Chapter 2: Covariates of Walleye *Sander vitreus* recruitment to age-0 from stocked populations in six Midwestern Reservoirs

Abstract: Walleye *Sander vitreus* are native to central North American freshwater habitats. Introductions within and outside their native range have occurred in all of the lower 48 states. These stockings have occurred due to the increasing popularity of this species leading to the demand surpassing the supply. Despite the popularity of this species for anglers and extensive research on the distribution, life history, population dynamics, culture, and stocking strategies, there is a paucity of information on first year survival of stocked populations. This is largely due to Walleye survival in a variety of habitats. The objective of this study was to test for associations between biotic and abiotic variables for Walleye recruitment to age-0 in the fall. We tested for the influence of distributional stocking patterns, moronid stocking abundance, spring/summer warming rate, and spring/summer maximum discharge on electrofishing catch rates in the fall of age-0 Walleye. We used a Bayesian hierarchical generalized linear model with the Poisson distribution to evaluate these relationships. Our model suggested the number of stocking events, moronid stocking abundance, and maximum discharge/rainfall were the most important factors influencing Walleye recruitment. This study will assist managers locally and regionally determine stocking strategies for Walleye as well as potential competitors to improve recruitment.

Key words: stock-recruitment; Indiana; modeling; Bayesian; hierarchical

INTRODUCTION

Walleye *Sander vitreus* are native to much of central North America in freshwater habitats (Scott and Crossman 1973) and introductions within and outside their native range have occurred in all of the lower 48 states (Fuller 2010). These introductions have continued for over a century in the United States in an effort to expand fishing opportunities (Lathrop et al. 2002), rebuild depleted stocks (MacDougall et al. 2007), supplement or enhance the fishery (Mathias et al. 1992), and mitigate poor year classes from variable natural recruitment (Johnson et al. 1996).

Walleye have historically been an important recreational and commercial species with demand surpassing supply. In 2011, they ranked seventh in overall angler preference for a species (U.S. Department of the Interior 2011). During that time, a total of 2.6 million anglers spent 39.1 million days fishing for Walleye (U.S. Department of the Interior 2006). Overall anglers spent an average of 15 days fishing for walleye.

Despite the popularity of Walleye, there is a paucity of information on factors governing first year survival of stocked populations. Walleye are capable of surviving in a variety of habitats (Bozek et al. 2011), resulting in a wide array of factors that can influence their first year survival (Forney 1976; Madenjian et al. 1996), including: size at stocking (Olsen et al. 2000), stocking density (Johnson et al. 1996), time of stocking (Donovan et al. 1997), warming rate of water (Quist et al. 2003), discharge (Willis and Stephen 1987), competition (Raborn et al. 2004) and predation (Quist et al. 2003).Yet, variability in these confounding factors and discrepancies in results suggest definitive conclusions on general trends are difficult, if not impossible to make. Thus, successful management of this species requires region specific evaluation and potentially lake specific observations. Further, while much is known about Walleye recruitment in states such as Nebraska, Wisconsin, and Kansas (Kempinger and Carline 1977; Serns 1982; Beard et

al. 2003; Nate et al. 2003; Quist et al. 2003; Quist et al. 2004; Quist et al. 2010; Uphoff et al. 2013; Fayram et al. 2014; Waterhouse et al. 2014) little is known in other states. Filling this information gap can help establish consensus on what factors contribute most to successful Walleye recruitment within and outside its native range.

Although native to Indiana, Walleye have been stocked in this state since 1891 (Andrews et al. 1994). Up to the late 1980s, management decisions on where to stock were based on public access, potential as a future brood stock source, and proximity to the rearing hatchery (Andrews et al. 1994). In 1987, a committee was formed to evaluate biotic and abiotic factors that could potentially influence successful establishment or continuation of the fishery (Andrews et al. 1994). Currently, these fisheries are supported by a program that consists of annual stockings. In 2014, 27.9 million fry and 870,000 fingerlings were stocked throughout the state (Dan Carnahan, Personal Communication). Despite this large annual commitment to stocking, much is still unknown about what factors are determining Walleye recruitment success in Indiana reservoirs.

The primary objective of this study was to use long-term data collected by the Indiana Department of Natural Resources to determine whether age-0 Walleye recruitment to the fall is associated with selected biotic and abiotic conditions. Specifically, we sought to determine the influence of Walleye distributional stocking patterns, moronid stocking abundance, spring/summer warming rate, and spring/summer maximum discharge on fall electrofishing catch rates of age-0 Walleye. We hypothesized that Walleye distributional stocking patterns and spring/summer warming rate will be positively associated, while moronid stocking abundance and spring/summer discharge will be negatively associated with fall electrofishing catch rates of age-0 Walleye.

METHODS

Study Area and stocking program

We studied recruitment of stocked Walleye to the fall at six reservoirs in southern Indiana (Figure1). Reservoirs ranged in area from 338 to 4,350 hectare and the shoreline development factor (SDF; Wetzel 2001), a measure of shoreline complexity, ranged from 2.59 to 10.67 (Table 1). The SDF is a ratio of the actual perimeter of the reservoir to the expected perimeter of a perfect circle with the same area. Average depth ranged from 5.5 m (Prairie Creek) to 9.1 m (Brookville; Table 1). Maximum depth ranged from 9.8 m (Prairie Creek) to 35.4 m (Brookville; Table 1). Summit Reservoir is the smallest by volume in our study while Monroe Reservoir is the largest (Table 1).

Monroe Reservoir was impounded in 1965 and operated by the Army Corps of Engineers for flood control. It is the largest reservoir in Indiana and has the most complex shoreline in this study. Monroe Reservoir is also the primary water supply for the City of Bloomington, IN. The reservoir has ten publicly owned boat ramps and several privately-owned recreational facilities. The Monroe Reservoir watershed is 114,219 hectares and consists primarily of deciduous forest (72%) and open water (17%; Table 2). Primary forage fishes consists of Gizzard Shad *Dorosoma cepedianum* and Bluegill *Lepomis macrochirus*. Predators include Largemouth Bass *Micropterus salmoides*, Walleye, Yellow Bass *Morone mississippiensis*, Smallmouth Bass *Micropterus dolomieu*, and hybrid Striped Bass *Morone chrysops x M. saxatilis*. During this study, Walleye fingerlings were stocked at an average rate 99 fish hectare^{-1} (standard error = 7; Table 2).

Brookville Reservoir was impounded during the winter of 1974-75 and also has a complex shoreline in relation to the remaining five reservoirs. The reservoir's primary function is flood control operated by the Army Corps of Engineers, yet it sits in the middle of a 6,655

hectare state park. The watershed is primarily cultivated crops (49%) and deciduous forests (25%), with smaller amounts that are developed (13%) or in pasture/hay (9%; Table 2). Primary forage fish consists of gizzard shad and bluegill. Predators include Largemouth Bass, Smallmouth Bass, Walleye, Striped Bass *Morone saxatilis*, White Bass *Morone chrysops*, and Muskellunge *Esox masquinongy*. Brookville Reservoir is the only brood stock source of Walleye for the Indiana Division of Fish and Wildlife. During this study, Walleye fry have been stocked at an average rate 5,458 fish hectare^{-1} (standard error = 267.2; Table 2).

Patoka Reservoir was impounded in 1977 and has the most complex shoreline in the reservoirs included in this study. The lake is managed for flood control by the Army Corps of Engineers, and for water supply by the Patoka Reservoir Regional Water and Sewer District that distributes water from the lake to 11 southern Indiana counties. The watershed is approximately 6,960 hectares of forested land. The Patoka Reservoir watershed consists primarily of deciduous forests (65%), pasture/hay (12%), and open water (8%; Table 2). Primary forage consists of Gizzard Shad and Bluegill. Predators include Largemouth Bass, Walleye, Striped Bass, Smallmouth Bass, and White Bass. During this study, Walleye fry were stocked at an average rate 1,212 fish hectare^{-1} (standard error = 306.4; Table 2).

Cagle's Mill Reservoir was built in 1952 as Indiana's first flood control reservoir operated by the Army Corps of Engineers, and has one of the least complex shorelines in this study. The 567 hectare lake is contained in a 3,268 hectare State Recreation Area. The Cagle's Mill watershed consists primarily of cultivated crops (61%), deciduous forests (23%), and pasture/hay (8%; Table 2). Primary forage fish consists of Gizzard Shad and Bluegill. Predators include Largemouth Bass, White Bass, and Walleye. During this study, Walleye fry were stocked at an average rate 5,293 fish hectare^{-1} (standard error = 665.4; Table 2).

Prairie Creek Reservoir is a 507 hectare water supply reservoir serving the city of Muncie, Indiana and has the least complex shoreline of this study. Indiana American Water Company manages the discharge from this reservoir. The surrounding land is managed by the Muncie Park and Recreation Department. The Prairie Creek Reservoir watershed consists primarily of cultivated crops (64%), open water (12%), and deciduous forests (9%; Table 2). Primary forage species include Gizzard Shad, Bluegill, Yellow Bass, and Yellow Perch *Perca flavescens*. Predators include Largemouth Bass, Smallmouth Bass, White Bass, and Walleye. During this study, Walleye fingerlings were stocked at an average rate 116 fish hectare^{-1} (standard error = 4.9; Table 2).

Summit Lake was impounded in 1981 and is one of two lakes in this study where the water levels are not operated by the Army Corps of Engineers. The discharge of Summit Lake is a fixed overflow and is not regulated by the State Park. The lake is surrounded by a 747 hectare State Park that was established in 1988. The Summit Lake watershed consists primarily of cultivated crops (49%), pasture/hay (19%), open water (13%), and deciduous forests (10%; Table 2). Primary forage fish include Bluegill, Redear Sunfish, and Yellow Perch. Predators include Largemouth Bass and Walleye. Walleye were introduced in 1999 to reduce the overabundant yellow perch population (Smyth 2008). Summit Lake is the only lake in this study that does not contain Gizzard Shad. During this study, Walleye fingerlings were stocked at an average rate 63 fish hectare^{-1} (standard error = 1.7; Table 2).

Fish Collection

Walleye were collected during September or October at all reservoirs using nighttime pulsed DC electrofishing with two dippers. Sampling effort ranged from 1.75 to 8.00 hours per

year, depending on lake size, with individual sampling stations consisting of 15 minutes of continuous electrofishing moving along the shoreline. Sample sites were the same each year. All Walleye captured were measured for total length and weight, and scales were removed for age and growth analysis.

Data

Age-length keys were created for each reservoir and year and used to assign ages to unaged Walleye. Abundance of age-0 Walleye was converted to catch per one hour of electrofishing and rounded to the nearest whole number for modeling.

Stocking events in each reservoir were conducted in the spring and the exact time was dependent on weather. Number of stocking events for any given reservoir and year are the sum total of individual stocking events. For example, if fish were hauled to the reservoir in one hatchery truck and stocked at a single location that would be a single event. If the stocking was spread across multiple days or locations that would represent multiple events (summed number of locations and days). Stocking was typically completed during May or June, but was weather dependent, often being delayed during periods of high discharge. If there was more than 2.8°C difference between truck tank water and receiving water, the tank water was allowed to acclimate prior to the fish release.

Moronids were only stocked at three locations: Monroe Reservoir (hybrid striped bass), and Brookville and Patoka reservoirs (Striped Bass). For the purposes of this analysis we did not differentiate between hybrid striped bass and Striped Bass. Any ecological effect (e.g., competition) was assumed to be similar. Moronids were not stocked into Cagle's Mill Reservoir, Prairie Creek Reservoir, or Summit Lake.

Warming rate (daily change in temperature) was calculated using data from the US Army Corps of Engineers and the Midwest Regional Climate Center (http://mrcc.isws.illinois.edu/CLIMATE/; accessed June 2014). Temperature profiles by water depth were acquired from the US Army Corps of Engineers, Louisville District for Monroe, Brookville, Patoka, and Cagle's Mill reservoirs. Three to five temperature profiles were recorded each month. Because historic temperature data at Prairie Creek Reservoir and Summit Lake were not available, we used air temperature from the nearest weather station (Table 3) in lieu of water temperature in the model. Warming rate was calculated as the slope of temperature at 1.5 m depth vs. days starting from the first recorded day in May to the last recorded day in July. Warming rate was calculated as the slope of average daily air temperature vs. days starting from the first recorded day in May to the last recorded day in July.

Discharge data were obtained from the US Army Corps of Engineers and the Midwest Regional Climate Center (http://mrcc.isws.illinois.edu/CLIMATE/; accessed June 2014). Outflow discharge (m^3 sec^{-1}) data were obtained from the US Army Corps of Engineers, Louisville District, for Monroe Reservoir, Brookville Reservoir, Patoka Reservoir, and Cagle's Mill Reservoir. Three to four measurements were recorded daily at each reservoir. We restricted the range of days in this study beginning with the last stocking days (between May and June) and ending in September to correlate with the time young-of-the-year fish were most vulnerable to outflows. While this potentially eliminates discharge information during stocking we only wanted to consider discharge events that would influence the complete year class. All reservoirs except Monroe were stocked before June 1 each year. No discharge data at Prairie Creek Reservoir and Summit Lake were available. Instead, we acquired precipitation data from the Midwest Regional Climate Center (Table 3) and used the maximum daily rain total (mm day^{-1})

as a proxy for daily discharge. The periods used were determined similarly as outflow discharge for the other water bodies.

All covariates were standardized to their z-scores using the following equation:

$$\text{Equation 1:} \quad \text{standard}(x_{ki}) = \frac{x_{ki} - \text{AVG}(x_k)}{\text{STD}(x_k)}$$

Where x_k is covariate k, x_{ki} is covariate k for individual i, AVG(x_k) is the average value of covariate k, STD(x_k) is the sample standard deviation for covariate k. Some data were missing for warming rates at Brookville (5 out of 20) and Monroe (1 out of 9) reservoirs, as well as, discharge at Monroe Reservoir (2 out of 20). Rather than omitting the entire yearly observation for missing individual data points, data were imputed following Gelman and Hill (2007) and Gelman et al. (2004). Here we assume the missing-data mechanism that generated the missing values was missing at random. We use a data imputation method which generates plausible values based on real data. The independent variables that have missing values (e.g., warming rate and discharges) were modeled as a normal distribution and the parameters of these distributions were used to generate random values for the missing data at each iteration of MCMC chain.

Model

Catch-per-unit-effort (CPUE) of age-0 Walleye was modeled using a hierarchical generalized linear model framework with a Poisson distribution. Lakes were initially separated based on data source for discharge and warming. Because Monroe, Brookville, Patoka, and Cagle's Mill reservoirs had historic discharge and water temperature data and Prairie Creek Reservoir and Summit Lake had a proxy (daily rain total and air temperature), they were modeled separately. This allowed us to eliminate variation that could be attributed to the data source rather than the actual affect. Thus, equation 2-3 included data from Monroe, Brookville,

Patoka, and Cagle's Mill reservoir while equation 4-5 included data from Prairie Creek Reservoir and Summit Lake. Additionally, equation 2-3 included moronids as a covariate while Equation 4-5 did not. Since Cagle's Mill Reservoir did not receive annual moronid stocking, the coefficient for moronids was set to zero. Thus, equation 2-3 includes covariates for number of stocking events (X_1), warming rate (X_2), discharge (X_3), and moronids (X_4). Reservoir was treated as a random effect in both models.

Equation 2: $$C_i|\mu_i \sim Poisson(\lambda_i)$$

Equation 3: $$\lambda_i = \alpha_j + \sum_{k=1}^{4} \beta_{kj} X_{kj}$$

Where C_i is the CPUE of age-0 Walleye for observation i, λ_i is the Poisson mean CPUE of observation i, β_{kj} is the coefficient for covariate k and lake j, and X_{kj} is covariate k for lake j. Equation 4-5 is analogous to equation 2-3 except covariates only loop through the first three covariates (i.e., stocking events, warming rate, and discharge).

Equation 4: $$C_i|\mu_i \sim Poisson(\lambda_i)$$

Equation 5: $$\lambda_i = \alpha_j + \sum_{k=1}^{3} \beta_{kj} X_{kj}$$

The hierarchical models were structured so that parameters for each reservoir were drawn from the same probability distribution. That is, reservoirs were treated as a random effect for each parameter. For Monroe, Brookville, Patoka, and Cagle's Mill reservoirs the priors for β_{1j}-β_{3j} where j = 1 through 4 are:

Equation 6: $$\beta_{1j} \sim normal(\mu_1, \sigma_1^2)$$

Equation 7: $$\beta_{2j} \sim normal(\mu_2, \sigma_2^2)$$

Equation 8: $$\beta_{3j} \sim normal(\mu_3, \sigma_3^2)$$

Prairie Creek Reservoir and Summit Lake coefficients are drawn from a different distribution than the others for β_{1j}-β_{3j} where j = 5 through 6 such that:

Equation 9: $\beta_{1j} \sim normal(\mu_4, \sigma_4^2)$

Equation 10: $\beta_{2j} \sim normal(\mu_5, \sigma_5^2)$

Equation 11: $\beta_{3j} \sim normal(\mu_6, \sigma_6^2)$

Where $\mu_{1\text{-}6}$ are given independent non-informative normal priors and $\sigma^2_{1\text{-}6}$ are given independent minimally-informative folded t-distribution priors following Kruschke (2011). Thus, the model has group level hyper-priors for Monroe, Brookeville, Patoka, and Cagle's Mill reservoirs, and separate hyper-priors for Prairie Creek Reservoir and Summit Lake. The last coefficient for the effect of moronid stocking were group level hyper-priors for Monroe, Brookville, and Patoka reservoirs (for j = 1 through 3) such that:

Equation 12: $\beta_{4j} \sim normal(\mu_7, \sigma_7^2)$

Where μ_7 is given independent non-informative normal priors and σ^2_7 is given independent minimally-informative folded t-distribution priors following Kruschke (2011).

All possible combinations of model parameters were evaluated and the most parsimonious model was selected by a deviance based loss function (Plummer 2008). The penalized deviance adds a greater penalty for complex models compared to deviance information criteria (DIC). The increased penalty is preferred when the number of observations does not greatly exceed the number of observations.

Bayesian Inference

We used Bayesian inference in R 3.1.1 (R Core Team 2014) using JAGS 3.4 (Plummer 2003) and rjags 3.13 (Plummer 2014) to estimate parameters of the model. All parameters were

given non-informative priors unless otherwise specified. Three concurrent MCMC chains were run and we used 100,000 saved steps thinning every 3 steps and discarding the first 50,000 steps. Convergence of the MCMC chains were checked using the Brooks-Gelman-Rubin (BGR) scale-reduction factor (Brooks and Gelman 1998). The BGR factor is the ratio of between-chain variability to within-chain variability. The chains converge when the upper limits of the BGR factor are close to one. Values less than 1.1 suggest the MCMC chains converged. Posterior distribution of the parameter estimates were described with medians and 95% credible intervals. Complete model specification using JAGS code is available upon request.

RESULTS

Brookville had the most year classes in our dataset (n = 20; Table 1) while Patoka had the fewest (n = 5; Table 1). Fall electrofishing catch rates of age-0 Walleye were variable across reservoirs ranging from 3 fish hour^{-1} at Summit Lake to 145 fish hour^{-1} at Monroe Reservoir (Table 3). Variability in catch rates was proportional to abundance with Summit Lake having the lowest standard error (SE = 1.2) and Monroe Reservoir having the highest (SE = 55.9). Average number of annual Walleye stocking events ranged from 3 (SE = 0.3) at Cagle's Mill and Prairie Creek Reservoir to 12 (SE = 1.2) at Monroe (Table 3). In contrast, stocking events were most variable at Patoka Reservoir (SE = 1.6). Moronid stockings ranged from 16 fish hectare^{-1} year^{-1} at Patoka to 25 fish hectare^{-1} year^{-1} at Brookville. The average warming rate was lowest at Summit Lake (0.13°C day^{-1}) and highest at Brookville Reservoirs (0.22°C day^{-1}; Table 3). Average discharge at Brookville Reservoir was the highest while Patoka Reservoir was the lowest (Table 3). Average rainfall ranged from 48 mm day^{-1} at Prairie Creek Reservoir to 59 mm day^{-1} at Summit Lake (Table 3).

All candidate models converged and the Brooks-Gelman-Rubin statistics, $\hat{R}$, was less than 1.1 for all parameters. Model selection criteria indicated the best model included the number of stocking events, moronid stocking abundance, and maximum discharge (Table 4). The top three models included some combination of the factors included in the best model. Temperature was included in the fourth ranked model.

The effect of Walleye stocking events was not concordant across all reservoirs (Figure 2). Stocking events were positively associated with CPUE at age-0 at Monroe Reservoir, Cagle's Mill Reservoir, and Summit Lake (Figure 2). As Walleye stocking events increased and with all other variables held constant at their average, the predicted increase in Walleye CPUE at age-0 increased most at Monroe Reservoir with smaller increases expected at Cable's Mill Reservoir and Summit Lake (Figure 3). See Table 3 for average values used. However, the coefficients for the remaining reservoirs overlapped 0, suggesting other variables influenced recruitment success.

The effect of moronid stocking abundance was also not concordant across all reservoirs (Figure 2). Moronid stocking abundance was negatively associated with Walleye CPUE at age-0 at Monroe and Patoka reservoirs while they were positively associated at Brookville Reservoir (Figure 4). Posterior predictions of Walleye CPUE at age-0 with average discharge and average stocking events had a strong negative response for Monroe Reservoir, a small but positive response at Brookville Reservoir, and no effect at Patoka Reservoir (Figure 5).

The effect of discharge on CPUE at age-0 was also not consistent across reservoirs (Figure 6). Walleye CPUE at age-0 was positively related to maximum discharge at Patoka and Cagle's Mill reservoirs and negatively related at Monroe and Brookville reservoirs (Figure 6). There was no relationship between Walleye CPUE at age-0 and maximum rainfall at Prairie Creek Reservoir and Summit Lake. However, there was high uncertainty in the estimates at

Patoka Reservoir and Summit Lake (Figure 6). An increase in discharge is predicted to decrease Walleye CPUE at age-0 most at Monroe Reservoir when moronid stocking and stocking events were at their average level (Figure 7).

DISCUSSION

This study evaluated Walleye recruitment dynamics from stocking to fall electrofishing CPUE at age-0. Our Bayesian hierarchical model permitted the inclusion of complex relationships between biotic and abiotic factors with fall electrofishing catch rates at multiple reservoirs in one modeling framework. The most parsimonious model describing Walleye recruitment to the fall included the number of stocking events, moronid stocking abundance, and maximum discharge/rain fall. Warming rate did not appear to influence Walleye recruitment. Our hypothesized relationships were consistent with some reservoirs while the directional relationship with one factor, maximum discharge/rain, was different among the reservoirs.

We are unaware of any study that evaluated Walleye stocking distributional patterns on stocking success, thus our study is the first to conclude this relationship. Our models predicted an increase in fall electrofishing CPUE at age-0 as stocking locations increased at three reservoirs (Figure 2). This could be explained by the limited dispersal of Walleye fingerlings post-stocking (Parsons and Pereira 1997). Thus, local perturbations at stocking could result in substantial loss of the initial cohort if few sites are stocked. Stocking distributional patterns have been associated with survival of other species whose population is dependent solely on stocking (i.e., Striped Bass, Sutton et al. 2013). However, Sutton et al. (2013) found an increase in survival as stocking abundance per site increased rather than a direct correlation with the number of sites stocked. Although, their case study resulted in a strong negative correlation between abundance stocked

per site and the number of stocking sites (i.e., as the number of stocking sites increased the number stocked per site decreased; Table 1 in Sutton et al. 2013).

We excluded the number of fish stocked as an explanatory variable for two reasons. First, stocking abundance is a poor explanatory variable for Walleye stocking success (Parsons et al. 1994; Johnson et al. 1996). The effect of high stocking abundance had no relationship with year-class strength in Minnesota (Parsons et al. 1994) and Wisconsin (Johnson et al. 1996). Second, the variability in stocking abundance at the reservoirs in our study was low. When stocking abundance was a significant contributor to recruitment, stocking abundance varied substantially (e.g., 0 to 60,770 fish/ha; Carlander and Payne 1977).

The negative relationship we observed between moronid stocking abundance and Walleye CPUE at age-0 could be explained by competitive effects. However, we did not test for direct competition between these fishes. Negative effects from competition in artificial systems can occur when there is limited time allowed to develop niche partitioning. Hence, we suggest this may result in variable levels of competition as the fishes in our study are top predators and have significant diet overlap (Raborn et al. 2004). For competition to occur between two species the exploited resource must be in limited supply. While this can be difficult to establish there is some evidence that this occurs in reservoirs in the spring (Crowder and Binkowski 1986; Fausch and White 1986). Further, significant diet overlap between Walleye and Striped Bass has been found in other reservoirs (Raborn et al. 2004), suggesting exploitive competition for shared resources could occur. In exploitative competition, one species uses the resource more quickly than the other. Young-of-the-year Walleye shift to piscivory as early as 30 mm (Jackson 1992). After this shift they are dependent on small cyprinid and age-0 fishes for prey (Forney 1974; Jackson et al. 1992). Jackson et al. (1992) found that prey size did not exceed 60 mm for age-0

Walleye even when Walleye reached 200 mm. This suggests that age-0 Walleye have a gape limitation for adult Gizzard Shad. While moronids do not share the same gape limitation and can consume clupeids up to 60% of their own length, although they typically forage on much smaller fish (Manooch 1973). Additionally, Sutton and Ney et al. (2001) found that age-0 Striped Bass in a Virginia Reservoir consumed alewives over 100 mm. Therefore, competition during early spring when age-0 Gizzard Shad abundance is low may explain the negative relationship we observed at two reservoirs. Future studies should monitor prey species abundance to assess the potential for an effect of prey abundance on stocking success.

The negative effect of discharge at two of our study reservoirs was not unexpected. In Kansas reservoirs, stocking success was positively related to storage ratios (Willis and Stephen 1987). Storage ratios are a ratio of reservoir volume to average annual discharge, where a high storage ratio indicates less turnover (i.e., lower discharge rate). In a similar assessment in rivers (Mion et al. 1998), survival of larval Walleye was inversely related to discharge.

Our results suggest that spring warming rate did not contribute to fall recruitment of Walleye. Quist et al. (2003) also found no relationship with spring warming rate in stocked systems, but their study was based on air temperature. In contrast, spring warming rate was related to recruitment in natural systems, (Madenjian et al. 1996), and appears to be more important during early life stages of Walleye in this environment.

Other factors not included in our model that contribute to a variable relationship with Walleye survival and growth including: initial conditions at stocking, size, abundance, and time of year (Johnson et al. 1996; Donovan et al. 1997; Olsen et al. 2000). For example, an evaluation of Walleye stocked as small (30-50 mm) and large (120-140 mm) fingerlings did not result in significantly different fall electrofishing catch rates in four New York State lakes (Olson et al.

2000). While this study suggested stocking larger fingerlings later in the season did not necessarily result in increased first year survival, Olson et al. (2000) could not identify the influence of naturally recruited individuals, while Madenjian et al. (1991) found stocking Walleye fingerlings at 60 mm rather than 50 mm tripled survival. Some evidence suggests initial stocking density is not an important variable to predict survival (Johnson et al. 1996). However, Fayram et al. (2005) found the relationship between stocking density and age-0 recruitment follows a Ricker model. Thus, density-dependent mechanisms can result in decreased survival. Finally, stocking time that coincides with their targeted food sources, such as the Gizzard Shad hatch, does result in increased survival (Quist et al. 2004; Zweifel et al. 2009).

Our model could not account for autocorrelation in the response and explanatory variables. For example, temporal autocorrelation among years in abiotic and biotic covariates was not assessed because we did not have consistent yearly data, a mandatory requirement (Barnett 2004). Temporal autocorrelation can result in naturally reproducing populations in stock-recruitment curves that describe a population that is more productive than reality (Hilborn and Walter 1992). While our study system was not dependent on natural reproduction, temporal autocorrelation could result in increased uncertainty in our parameter estimates. This limitation highlights the importance of consistent long-term monitoring programs.

Management Implications

Our research suggests recruitment of age-0 Walleye to the fall can be increased by increasing the number of stocking events in any given year. In large reservoirs with many access sites, stocking can occur on the same day with minimal extra effort to distribute the fish. In small reservoirs with few access sites the best option would be to make multiple trips to the reservoir

and stock the same sites on different days. This modification should be considered in all Walleye stocking programs where feasible.

Secondly, our research suggests that fall recruitment of age-0 Walleye is influenced by the number of stocked moronids. Reducing the stocking abundance of moronids would yield significant improvements in Walleye recruitment; however, additional input from the public should be attained before eliminating a stocking program for potential competing species. Further, stock-recruitment relationships for moronids should be evaluated to determine whether a fishery could be maintained at reduced stocking abundance which would then benefit Walleye recruitment.

Finally, our research suggests that fall recruitment of age-0 Walleye is influenced by discharge. Unfortunately, regulation of discharge is often not in the control of the fisheries managers nor is the weather. In our case, most of the reservoirs we studied are operated by the Army Corps of Engineers and discharge is regulated to minimize flooding. Thus, while discharge should be considered when trying to predict future success, it is not a variable that can be readily manipulated. The stocking program would benefit by avoiding stocking Walleye during periods of high discharge. For example, if adequate storage facilities exist fish should be held until flooded reservoirs are drawn down to normal levels.

Chapter 3: Yield-per-recruit of competing piscivores in a Midwestern Reservoir

Abstract: Reservoir fisheries can consist of a variety of stocked predators which often overlap in their diet. Fisheries programs based on fish that are stocked annually, such as in many Midwestern reservoirs, are managed differently than naturally reproducing fisheries. With stocked fish, little regard is given to reproductive concerns, with significant effort directed towards estimation of growth and mortality to estimate yield. Understanding expected yield while acknowledging the uncertainty in life history parameter estimates can help managers determine the best harvest strategies to improve angler success. To that end, our objective was to evaluate yield-per-recruit models of Walleye *Sander vitreus* and hybrid Striped Bass *Morone chrysops x M. saxatilis* under variable harvest strategies (e.g., variable minimum length limits and exploitation) and three levels of conditional natural mortality (cm = estimated natural mortality, 0.20, and 0.50). Yield estimates of both species were sensitive to specification of conditional natural mortality. Specifically, we showed that Walleye yield would increase if the minimum size limit was increased under moderate to low conditional natural mortality and moderate to high exploitation. In contrast, hybrid Striped Bass yield would be expected to increase with an increase in the minimum size limit with two conditions. The results provide insight on the expected yield under different minimum size limits and bag limits while incorporating uncertainty in the model inputs as well as add to the sparse literature on hybrids striped bass population dynamics.

Key words: Walleye, hybrid striped bass, yield-per-recruit, growth, mortality

INTRODUCTION

Reservoir fisheries can consist of a variety of stocked predators including Rainbow Trout *Oncorhynchus mykiss*, Northern Pike *Esox Lucius*, Largemouth Bass *Micropterus samloides*, Walleye *Sander vitreus*, Striped Bass *Morone saxatilis* and hybrid striped bass *Morone chrysops x M. saxatilis* (Rahel 2000; Bulak et al. 2013) which often overlap in their diet (Miranda and Raborn 2013; Raborn et al. 2004). Decisions on how many and which species to stock are frequently based on forage abundance (i.e., Gizzard Shad *Dorosoma cepedianum*) and angler opinion (McMullin 1996; Churchill et al. 2002; Arlinghaus and Mehner 2005). As a result, the species stocked can often lead to competing interests among the anglers (Churchill et al. 2002) and competition between stocked piscivores can affect their growth, mortality, and yield (Kennedy and Strange 1986; Raborn et al. 2004; Fayram et al. 2005; DeBoer et al. 2013).

Fisheries programs based on fish that are stocked annually, such as in many Midwestern reservoirs, are managed differently than naturally reproducing fisheries. With stocked fish, little regard is given to reproductive concerns, with significant effort directed towards estimation of growth and mortality. By controlling fishing mortality, it is often possible to create desirable harvested lengths or weight yields. This approach maximizes yield (Beverton and Holt 1975), often expressed as yield per recruit (Ricker 1975). That is, predicting the expected yield (kg) for a specific number of recruits while taking into account growth and mortality. Quantification of yield can be difficult with reservoir fisheries, as competitive interactions influencing yield are assumed, but not well defined. Thus, investigating expected yield of competing species is necessary to fully understand the implications of variable size and regulatory limits.

Growth, mortality, and yield can be influenced by biotic and abiotic factors (Kershner et al. 1999). Biotic factors, such as abundance of forage fish (Quist et al. 2003), can be indirectly

controlled by the manager by altering the stocking abundance of competing predators. However, abiotic factors, such as water temperature (Serns 1982; Quist et al. 2002) and discharge (Mion et al. 1998) typically cannot be controlled. Nevertheless, these factors produce uncertainty in estimates of growth and mortality parameters that is often ignored when evaluating yield-per-recruit models. Ignoring this uncertainty and treating yield-per-recruit input variables as fixed can result in erroneous conclusions, particularly with yield estimations. Therefore, to reduce the chances of committing type-1 error, the manager must consider all sources of variation when determining expected yield.

Although Walleye and hybrid striped bass have been heavily studied (Barton 2011; Bulak et al. 2013), to our knowledge no effort has been made to incorporate uncertainty in estimates of growth and mortality into models predicting yield of these species. Jacobson (1996) evaluated a value-per-recruit analysis of Walleye using a modified Beverton-Holt dynamic pool model using point estimates for growth and mortality. Hoffman et al. (2013) used a Beverton-Holt yield-per-recruit model to estimate yield of hybrid striped bass; however, their simulations were based on one year of data and point estimates for growth and mortality parameters. Schultz and Dodd (2008) also used a Beverton-Holt yield-per-recruit model to estimate yield of Walleye and hybrid striped bass but also used point estimates for their model inputs. Thus, the influence of growth and mortality variation on yield of these species is unknown.

Understanding expected yield while acknowledging the uncertainty in life history parameter estimates can help managers determine the best harvest strategies to improve angler success. To that end, our objective was to evaluate yield-per-recruit models of Walleye and hybrid striped bass under variable harvest strategies (e.g., variable minimum length limits and exploitation) and three levels of conditional natural mortality (cm = estimated natural mortality,

0.20, and 0.50). To accomplish this we described age and growth, mortality, and weight-length relationships of both species and used the uncertainty in these estimates as model inputs for yield-per-recruit analysis. We hypothesized that yield of both species would increase with increased exploitation and increased length limit. We further hypothesized that yield will increase as conditional natural mortality decreases.

METHODS

Study Area

We studied population dynamics of Walleye and hybrid striped bass at Monroe Reservoir in south-central Indiana (Figure 8). Monroe reservoir is operated by the Army Corp of Engineers as a flood control reservoir and is the largest reservoir in Indiana at 4,350 hectares. The watershed land use consists of 74% deciduous forest, 17% open water, 4% pasture/hay, with the remaining land use (barren land, cultivated crops, developed land, wetlands, evergreen forest, and shrub/scrub) representing less than 2% each (Table 2). The fish community consists of Gizzard Shad, White Crappie *Pomoxis annularis*, Bluegill *Lepomis macrochirus*, Yellow Bass *Morone mississippiensis*, Longear Sunfish *Lepomis megalotis*, Channel Catfish *Ictalurus punctatus*, Largemouth Bass, Spotfin Shiner *Cyprinella spiloptera*, and hybrid striped bass (Kittaka 2008-A). Walleye fingerlings have been stocked annually since 1982 and hybrid striped bass fingerlings have been stocked annually since 1983. Since 2000, Walleye fingerlings have been stocked an average of 92 hectare^{-1} and hybrid striped bass fingerlings have been stocked an average of 17 hectare^{-1}. Walleye are managed with a 356 mm length limit and six fish bag limit while hybrid striped bass are managed with no minimum length limit, 12 fish bag limit, of which no more than two can exceed 432 mm.

Data Collection

Fishes were collected during the months of September and October using nighttime pulsed DC boat electrofishing with two dippers. Walleye sampling was conducted for eight years between 1994 and 2011, and hybrid striped bass sampling was conducted for seven years between 2004 and 2012. Thirty-two sites were sampled each year for 15 minutes each, creating an annual sampling effort of 8 hours. All fishes collected were identified and measured for total length. Total weight was recorded for up to four (when possible) individuals per 2.5 mm length class. Scales were removed for age and growth analysis and to provide the information necessary to generate age-length keys.

The data were used to evaluate a Beverton-Holt yield-per-recruit model. This model estimates yield (typically expressed as kg per 100 recruits) using parameters of the von Bertalanffy growth model, catch curve regression model, weight-length regression, and estimated natural mortality rate with a specified minimum length limit and exploitation. Typically multiple minimum length limits are evaluated as well as a range of exploitation to examine the effects of variable size and bag limits.

Age and Growth Models

Age and growth of both species were assessed by fitting a von Bertalanffy growth model to mean length-at-age (Equation 1; von Bertalanffy 1938) such that;

$$\text{Equation 1:} \quad y_i = L_\infty\left(1 - e^{-\kappa(age_i - t_0)}\right) + \varepsilon_i$$

$$\text{Equation 2:} \quad \varepsilon_i \sim normal(0, \sigma^2)$$

Where y_i is average total length (mm) of fish collected in year i, L_∞ is the hypothetical maximum total length achieved, κ is the Brody growth coefficient with units t^{-1}, age_i is the age of fish collected in year i, t_0 is the age when individuals would have been length 0, and ε_i is a random error term with mean 0 and constant variance σ^2 (Equation 2). To improve convergence of the model, we followed Kimura (2008) where L_∞, κ, and t_0 are estimated using a logarithmic scale. However, because negative values are possible for t_0, and by definition, would not be possible on the log scale, we added 10 to t_0. Ten was also subtracted from the t_0 parameter when interpreting the coefficient on the original scale. We additionally treated year of collection as a random effect for Walleye (i.e., pseudo-cohort) and year class as a random effect for hybrid striped bass. This allowed us to share information among years and generate a posterior distribution for each parameter used to create the yield-per-recruit model. Thus, each model parameter (L_∞, κ, and t_0) were index for j year of collection (Walleye) or year class (hybrid striped bass; Equation 3-5) such that:

$$\text{Equation 3:} \quad \ln(L_{\infty j}) \sim normal(mu_1, \sigma_1^2)$$

$$\text{Equation 4:} \quad \ln(\kappa_j) \sim normal(mu_2, \sigma_2^2)$$

$$\text{Equation 5:} \quad \ln(t_{0j}) \sim normal(mu_3, \sigma_3^2)$$

Where mu_1, mu_2, and mu_3 represent the overall mean L_∞, κ, and t_0 and σ^2_1, σ^2_2, and σ^2_3 represent the global precision for the model parameters.

Mortality Models

We used the hierarchical catch curve described by Doll and Lauer (2014) to estimate mortality parameters for both species (Equation 6). Here the traditional catch curve of Chapman and Robson (1960) is linearized by taking the natural log of both sides such that:

Equation 6: $\ln(C_i) = \ln(\alpha) - Z * age_i$

where C_i is the estimated catch at age i, α is the intercept, and Z is the slope interpreted as the instantaneous mortality rate. To estimate parameters, C_i is modeled using a Poisson distribution with the log link:

Equation 7: $C_{ij}|\lambda_{ij} \sim \text{Poisson}(\lambda_{ij})$

Equation 8: $ln(\lambda_{ij}) = \alpha_j - Z_j * age_{ij}$

where λ_{ij} is the Poisson mean for year class j at age i, α_j is the intercept for year class j, Z is the instantaneous mortality rate for year class j, and age_{ij} is the age i for year class j. Year class is treated as a random effect for both species where parameters for each year class follow a hierarchical structure such that they come from the same global distribution (Equation 9 and 10);

Equation 9: $\alpha_j \sim normal(\alpha_0, \sigma_0^2)$

Equation 10: $Z_j \sim normal(\beta_1, \sigma_z^2)$

where α_0 and $\beta_1$represent the overall intercept and slope (Z), and σ^2_0 and σ^2_z, represent the variation in the intercepts and slopes among year classes.

We used five methods to estimate a range of natural mortality values (M; Equation 11 – 15):

Equation 11: Quinn and Deriso (1999) $\text{M} = \frac{-\ln(\text{Ps})}{\text{t}_{\max}}$

Equation 12: Hoenig (1983) $\ln(\text{M}) = 1.46 - 1.01 * \ln(\text{t}_{\max})$

Equation 13: Jensen (1996) $\text{M} = 1.5 * \kappa$

Equation 14: Peterson and Wroblewski (1984) $\text{M} = 1.92 * \left(\text{W}_\infty{}^{-0.25}\right)$

Equation 15: Chen and Watanabe (1989) $\text{M}_{(t_i \text{ to } t_f)} = \left(\frac{1}{t_i - t_f}\right) * \frac{\ln\left(e^{\kappa * t_f} - e^{\kappa * t_0}\right)}{e^{\kappa * t_f} - e^{\kappa * t_0}}$

where Ps is the proportion of the population that survives to the maximum age (set to 0.01), t_{max} is the maximum age attained (set to 10 for Walleye and 13 for hybrid striped bass), t_i is the time of initial ages (set to 1), and t_f is the final age (set to 10 for Walleye and 13 for hybrid striped bass). To select a specific value for natural mortality we used the minimum and maximum calculated value from models 11-15 as the upper and lower bounds of a uniform distribution and a new value was randomly selected from this uniform distribution at each iteration of the yield-per-recruit model (see yield-per-recruit section for more details) Natural mortality was converted to conditional natural mortality (cm) using the following equation (Ricker 1975):

$$\text{Equation 16:} \quad \text{cm} = 1 - e^{-\text{M}}$$

Weight-Length Regressions

For the yield-per-recruit model to predict yield in terms of weight, length must be converted to weight. For this conversion we estimated parameters of the exponential relationship between weight and length using the following equations:

$$\text{Equation 17:} \quad \text{W}_i = \alpha + \text{L}_i\text{^}\beta + \varepsilon_{2i}$$

$$\text{Equation 18:} \quad \varepsilon_{2i} \sim normal(0, \sigma^2)$$

where W_i (g) is weight of individual i, L_i is the total length (mm) of individual i, α is the intercept, β is the slope, and ε_{2i} is a random error term with mean 0 and constant variance σ^2. We assumed this relationship was constant among year classes and analyzed all individuals regardless of year class as one model with one distribution estimated for α and β.

Bayesian Inference

Age and growth, mortality, and length-weight models were fitted using Bayesian inference in R 3.1.1 (R Core Team 2014) using JAGS 3.4 (Plummer 2003) and rjags 3.13 (Plummer 2014). Three concurrent MCMC chains were run for all models. The von Bertalanffy model consisted of 500,000 saved steps thinning every 3 steps and discarding the first 50,000 steps. The catch-curve model consisted of 100,000 saved steps thinning every 3 steps and discarding the first 10,000 steps. The length-weight model consisted of 100,000 saved steps thinning every 3 steps and discarding the first 10,000 steps. All parameters were given non-informative priors. Convergence of the MCMC chains was checked using the Brooks-Gelman-Rubin (BGR) scale-reduction factor (Brooks and Gelman 1998). The BGR factor is the ratio of between-chain variability to within-chain variability. The chains have converged when the upper limit of the BGR factor is close to one. Values less than 1.1 suggests the MCMC chains have converged. Posterior distribution of the parameter estimates are describe with their mean and standard deviation. Complete model specification using JAGS code is available upon request.

Yield-Per-Recruit Model

The Beverton-Holt yield-per-recruit model with Jones' modification (Model 19) was used to calculate yield-per-recruit curves for both species under variable harvest strategies (Beverton and Holt 1957, Jones 1957, Ricker 1975):

$$\text{Equation 19:} \quad Y = \frac{F * N_0 * e^{Fr} W_\infty}{\kappa} * (B[X, P, Q] - B[X_1, P, Q])$$

where Y is yield in g, F is the instantaneous rate of fishing, N_0 is the hypothetical number of individuals that reach age t_0 annually, t_0 is the hypothetical age at which the fish would have been zero length calculated from the von Bertalanffy model, r is the difference between age of recruitment to the fishery (t_r) and t_0, W_∞ is the average asymptotic weight of a fish calculated

using the length-weight equation and L_∞ from the von Bertalanffy model, κ is the Brody growth coefficient, *B* represents the incomplete beta function, and X, X_1, P, and Q are parameters of the incomplete beta function and calculated as follows:

$$\text{Equation 20:} \quad X = e^{-\kappa r}$$

$$\text{Equation 21:} \quad X_1 = e^{-\kappa(t_\lambda - t_0)}$$

$$\text{Equation 22:} \quad P = \frac{Z}{\kappa}$$

$$\text{Equation 23:} \quad Q = \beta + 1$$

where r and κ are as before, t_λ is the maximum age attained, Z is the instantaneous total mortality rate calculated with the mortality model above, and β is the slope from the length-weight equation. Instantaneous rate of fishing, F, was calculated as:

$$\text{Equation 24:} \quad \frac{(u * Z)}{(1 - S)}$$

where *u* is the exploitation rate (a specified value in the simulation) and S is the annual survival calculated by exponentiating Z. Age of recruitment to the fisheries, t_r, is calculated by inverting the von Bertalanffy growth model:

$$\text{Equation 25:} \quad t_r = \frac{\ln\left(1 - {}^{TL}/_{L_\infty}\right)}{-\kappa} + t_o$$

where TL is the harvest length being evaluated.

The yield-per-recruit model is typically calculated using fixed parameters estimated from the von Bertalanffy, catch curve model, natural mortality estimates, and length-weight model (Ragonese and Bianchini 1996; Jones and Wells 2001; Kirchner 2001). However, we took a Monte Carlo approach to estimate yield using random values for each model parameter (e.g., L_∞, t_0, β, etc.) so that at each Monte Carlo simulation step we acknowledged uncertainty in the model inputs. To accomplish this we used the Bayesian posterior distribution of the model parameters.

Random values for the natural mortality estimates were selected from a uniform distribution (see natural mortality section for more detail) while the remaining parameters were drawn from a normal distribution with the mean and standard deviation specified from the Bayesian inference results. To generate a range of plausible values for yield and incorporating the uncertainty in the model inputs, we calculated yield 1000 times and at each iteration, a new random value was generated for model parameters from their respective distribution.

Using the Monte Carlo simulations above, we estimated yield (kg) per 100 recruits of Walleye and hybrid striped bass under fixed and variable minimum length limits with a gradient of exploitation and conditional natural mortality. First, we estimated yield under three fixed minimum harvest length limits (356, 406, and 457 mm) and exploitation (u) ranging between 0.05 and 1.00 in 0.05 increments. The initial simulations use a calculated conditional natural mortality (cm), however, we also wanted to evaluate yield under low and high natural mortality. Thus, we also estimated yield with the three minimum harvest length limits, variable u, and cm fixed at 0.20 and 0.50. Second, we explored average yield estimates under a gradient of minimum length limits of 200 to 550 mm in 25 mm increments for Walleye and 200 to 600 mm in 25 mm increments for hybrid striped bass with exploitation rates (u) ranging from 0.05 to 1.00 in 0.05 increments. Uncertainty in the model estimates are expressed as 2 times the standard error.

RESULTS

Walleye: Parameter Values

Eight years of data were included in the Walleye von Bertalanffy growth model and treated as a pseudo-cohort. Mean (SD) Walleye L_∞ was 717 (43.05) (Table 5) and ranged from

666 in 2009 to 784 in 1994. There was a decreasing trend in Walleye L_∞ with year. Mean (SD) Walleye Brody growth coefficient (κ) was 0.245 (0.032) (Table 5) and κ for individual years ranged from 0.241 in 1998 to 0.252 in 2007.

Catch curve analysis of Walleye was limited to six year classes due to small sample size of older individuals. Overall mean (SD) instantaneous total mortality (Z) was -0.84 (0.157) (Table 5). This corresponded to mean (SD) total annual survival (S) and mortality (M) estimates of 0.43 (0.068) and 0.57 (0.068). Individual year class Z's ranged from -1.69 in 2004 to -0.43 in 2002.

Walleye natural mortality (M) estimates ranged from 0.25 (Peterson and Wroblewski 1984) to 0.46 (Table 6; Quinn and Deriso 1999; Chen and Watanabe 1989). These natural mortality estimates resulted in conditional natural mortality estimates (cm) used in the yield-per-recruit model that ranged from 0.22 to 0.37. To generate a random value for natural mortality in the yield-per-recruit model we used the upper (0.46) and lower (0.25) natural mortality (M) estimates as parameters of a uniform distribution. These distribution parameters resulted in resulted in natural mortality to average 0.36 and conditional natural mortality to average 0.30.

Four hundred and forty Walleye were used to estimate coefficients of the weight-length model. The intercept was $4.08 * 10^{-6}$ and slope was 3.14 (Table 5).

Walleye: Yield-Per-Recruit

Calculated conditional natural mortality = 0.30

Walleye yield varied with minimum length limits and exploitation rates using the calculated cm (0.30) according to the Beverton-Holt yield-per-recruit model. There were no differences in yield between the three minimum length limits (356, 406, and 457 mm) at low to

moderate exploitation ($u < 0.50$; Figure 9-A). However, at high exploitation ($u = 0.75$) estimated yield at 406 and 457 mm length limit was 13% and 15% lower at the minimum length limit of 356 mm. When evaluating a gradient of minimum length limits (200 to 550 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural mortality Walleye yield estimates ranged from 6 to 22 kg per 100 recruits (Figure 10). Maximum yield for Walleye was achieved when exploitation was approximately 0.55 and the minimum length limit was approximately 425 mm (Figure 10, 22 kg contour). Yield decreased to approximately 20 kg when high exploitation was coupled with a minimum length limit greater than 500 mm. In contrast, yield was maximized with intermediate exploitation rates between 0.25 and 0.50 when the minimum length limit was between 350 and 400 mm (Figure 10, 20 kg contour). Finally, yield remained constant at lower levels of exploitation (e.g., $u < 0.25$) with length limits between 250 and 500 mm (Figure 10). Growth overfishing is expected at minimum length limits below 300 mm; that is, fish are being harvested at an average size smaller than what would be produced at the maximum yield.

Conditional natural mortality = 0.20

Walleye yield varied with minimum length limits and exploitation rates using the cm of 0.20, according to the Beverton-Holt yield-per-recruit model. There were no differences in yield between the three minimum length limits (356, 406, and 457 mm) at low exploitation ($u < 0.25$; Figure 9-B). However, at moderate to high exploitation ($u > 0.25$) yield was consistently different (i.e., non-overlapping error bars) among the three minimum length limits. Specifically, at an exploitation rate of 0.75, estimated yield increased 17% from a minimum length limit of 356 to 406 mm and increased an additional 13% from 406 to 457 mm. When evaluating a

gradient of minimum length limits (200 to 550 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural mortality rate of 0.20, Walleye yield estimates ranged from 15 to 40 kg per 100 recruits (Figure 11). Maximum yield for Walleye was achieved when exploitation was approximately 0.35 and the minimum length limit was approximately 475 mm (Figure 11, 40 kg contour). Under high exploitation (e.g., $u >$ 0.50), yield was maximized when the minimum length limit was greater than 425 mm (Figure 11, 40 kg contour). In contrast, yield remained constant at lower levels of exploitation (e.g., $u <$ 0.25) with length limits greater than 300 mm (Figure 11). Growth overfishing is expected at minimum length limits below 350 mm.

Conditional natural mortality = 0.50

Walleye yield varied with minimum length limits and exploitation rates using the cm of 0.50 according to the Beverton-Holt yield-per-recruit model. Yield increased as the minimum length limits (356, 406, and 457 mm) decreased at all levels of exploitation (Figure 9-C). This indicates fish are being lost to natural mortality before they can be harvest. When evaluating a gradient of minimum length limits (200 to 550 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural mortality rate of 0.50 Walleye yield estimates ranged from 0.5 to 6.0 kg per 100 recruits (Figure 12). Maximum yield for Walleye was achieved when exploitation was approximately 0.90 and the minimum length limit was approximately 300 mm (Figure 12, 6.0 kg contour). Yield declines as the minimum length limit increases above 300 mm for all levels of exploitation (Figure 12). Growth overfishing is not expected with high levels of conditional mortality.

Hybrid Striped Bass: Parameter Values

Nine year classes were included in hybrid striped bass von Bertalanffy growth model. Individuals of older ages were removed due to low sample size. Mean (SD) L_∞ was 660 (20.07) (Table 6) and ranged from 654 in 2007 to 684 in 2008. Mean (SD) Brody growth coefficient (κ) was 0.410 (0.045) (Table 5) and κ for individual years ranged from 0.399 (2007) to 0.422 (2008).

Eleven year classes were included in the catch curve analysis of hybrid striped bass. Overall instantaneous mean (SD) total mortality (Z) was -0.45 (0.088) (Table 5). This corresponds to total mean (SD) annual survival (S) estimates of 0.64 (0.056) and total annual mortality (M) of 0.36 (0.056). Instantaneous total mortality for individual year classes ranged from -1.10 in 2004 to -0.20 in 1998.

Hybrid striped bass natural mortality (M) estimates ranged from 0.25 (Peterson and Wroblewski 1984) to 0.62 (Table 6; Jensen 1996). These natural mortality estimates resulted in conditional natural mortality estimates (cm) used in the yield-per-recruit model that ranged from 0.22 to 0.46. To generate a random value for natural mortality in the yield-per-recruit model we used the upper (0.62) and lower (0.25) natural mortality (M) estimates as parameters of a uniform distribution. These distribution parameters resulted in resulted in natural mortality to average 0.45 and conditional natural mortality to average 0.36.

Five hundred and seventeen hybrid striped bass were used to estimate coefficients of the weight-length model. The intercept was $1.00 * 10^{-5}$ and slope was 3.04 (Table 5).

Hybrid striped bass: Yield-per-recruit

Calculated conditional natural mortality = 0.36

Hybrid striped bass yield varied with minimum length limits and exploitation rates using the calculated cm (0.36) according to the Beverton-Holt yield-per-recruit model. There were no differences in yield between the three minimum length limits (356, 406, and 457 mm) at all levels of exploitation (Figure 13-A). When evaluating a gradient of minimum length limits (200 to 600 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural mortality hybrid striped bass yield estimates ranged from 5 to 35 kg per 100 recruits (Figure 14). Maximum yield for hybrid striped bass yield was achieved when exploitation was approximately 0.60 and the minimum length limit was approximately 450 mm (Figure 14, 35 kg contour). Yield decreased as the length limit increased above 500 mm and exploitation is greater than 0.60 (Figure 14). At low levels of exploitation ($u < 0.25$) yield remains constant for minimum length limits below 500 mm (Figure 14). Growth overfishing is expected with a 200 mm minimum length limit.

Conditional natural mortality = 0.20

Hybrid striped bass yield varied with minimum length limits and exploitation rates using the cm of 0.20 according to the Beverton-Holt yield-per-recruit model. There were no differences in yield between the three minimum length limits (356, 406, and 457 mm) at low exploitation ($u < 0.25$; Figure 13-B). However, at moderate to high exploitation ($u > 0.25$) yield was consistently different (i.e., non-overlapping error bars) between the three minimum length limits. Specifically, at an exploitation rate of 0.75, estimated yield increased 14% from a minimum length limit of 356 to 406 mm and increased an additional 10% from 406 to 457 mm. When evaluating a gradient of minimum length limits (200 to 600 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural

mortality rate of 0.20 hybrid striped bass yield estimates ranged from 20 to 75 kg per 100 recruits (Figure 15). Maximum yield for hybrid striped bass was achieved when exploitation was approximately 0.50 and the minimum length limit was approximately 500 mm (Figure 15, 75 kg contour). At high exploitation ($u > 0.50$) yield increases as the minimum length limit increase from 200 to 500 mm. In contrast, at low exploitation ($u < 0.25$) yield does not change with increasing minimum length limit (Figure 15). Growth overfishing would be expected when the minimum length limit is less than 400 mm.

Conditional natural mortality = 0.50

Hybrid striped bass yield varied with minimum length limits and exploitation rates using the cm of 0.50 according to the Beverton-Holt yield-per-recruit model. Yield increased as the minimum length limits (356, 406, and 457 mm) decreased at all levels of exploitation (Figure 13-C). This indicates fish are being lost to natural mortality before they can be harvested. When evaluating a gradient of minimum length limits (200 to 600 mm in 25 mm increments) and exploitation rates (0.05 to 1.00 in 0.05 increments) with the calculated conditional natural mortality rate of 0.50 hybrid striped bass yield estimates ranged from 2 to 14 kg per 100 recruits (Figure 16). Maximum yield for hybrid striped bass was achieved when exploitation was approximately 0.50 and the minimum length limit was approximately 300 mm (Figure 16, 14 kg contour). Yield declined as the minimum length limit increases above 400 mm for all levels of exploitation (Figure 16). At moderate to high exploitation ($u > 0.50$) yield declined from 14 to 2 kg as the minimum length limit increases above 400mm. Growth overfishing is not expected with high levels of conditional mortality.

DISCUSSION

This study used a Beverton-Holt yield-per-recruit model to estimate yield of Walleye and hybrid striped bass in a Midwestern reservoir based on variable harvest strategies, exploitation rates, and natural mortality while incorporating uncertainty from the model inputs. The models directly incorporated uncertainty in yield estimates by calculating yield through a series of iterations where model inputs were randomly selected from their posterior probability distribution. This approach improves the ability of a manager to assess uncertainty when comparing yield estimates that could not be evaluated if point estimates were used as model inputs. Using our data, yield estimates of Walleye and hybrid striped bass were sensitive to exploitation and specification of conditional natural mortality. Specifically, we showed that Walleye yield increases if the minimum size limit was increased under moderate to low conditional natural mortality and moderate to high exploitation. In contrast, hybrid striped bass yield would be expected to increase with an increase in the minimum size limit and one of two other conditions. First, if conditional natural mortality is at our calculated rate of approximately 0.36 and exploitation is greater than 0.65 and second, if conditional natural mortality is low (cm = 0.20) and exploitation is greater than 0.50. Finally, growth overfishing was found to be a possibility for both species except under conditions with high natural mortality. The results provide insight on the expected yield under different minimum size limits and bag limits while incorporating uncertainty in the model inputs as well as add to the sparse literature on hybrids striped bass population dynamics.

Yield-per-recruit models have been studied extensively by Beverton and Holt (1957), however, there is limited application of these model that explicitly incorporate uncertainty in model inputs. Most studies conducting yield-per-recruit analysis calculates yield based on point

estimates (Ragonese and Bianchini 1996; Jones and Wells 2001; Kirchner 2001). This is likely due to popular software that allows simple modification to input fixed values and calculates yield under a variety of specific minimum length limits, exploitation, and natural mortality (Splike and Maceina 2000). While this approach is common, the uncertainty in the estimates of model parameters is lost. We addressed this problem by using Bayesian inference to estimate a probability distribution for each Beverton-Holt model input. Thus, the distributional parameters (e.g., mean and standard deviation) that describe the model inputs are easily incorporated into a Monte Carlo simulation in order that random values can be generated at each iteration. This method provided estimates of yield with uncertainty that is based on the data and can provide managers with a more realistic expectation of yield. By incorporating known uncertainty in the parameters, managers can examine not only the general trend but also assess the degree of overlap or uncertainty in the estimates. Thus, managers are better able to identify changes or differences in yield. For example, when comparing point estimates of Walleye yield, there was a 10% difference in the mean yield estimates between a minimum size limit of 356 and 406 mm (Figure 9-A). However, the amount of overlap in the estimates is substantial (Figure 9-A), thus suggesting that there is no credible difference in the estimates.

The use of Bayesian inference to generate posterior distributions of the Beverton-Holt yield-per-recruit model inputs provides three advantages. First, the results are a posterior probability assessment of the model parameters (e.g., L_∞, t_0, β, etc.) that permit the incorporation of the estimated uncertainty into the yield-per-recruit model. Second, the hierarchical models estimate an overall distribution for the model parameters and one for each year or year-class. By doing this, the manager can evaluate year specific parameters and conduct post-hoc comparisons between the groups that do not relay on any form of correction for determining a significant

difference (Gelman et al. 2012). The group parameters, which have their individual mean and SD, can also be used in the yield-per-recruit model to evaluate the year or year-class specific yield-per-recruit model. Finally, prior information is easily incorporated within the Bayesian framework if data are limited or there is substantial knowledge about the system the manager wishes to directly incorporate into the analysis. This provides the manager with a suite of tools that can be applicable to their unique situation, particularly if the fishery contains multiple stocked species that share resources or there is limited information about their population dynamics.

Walleye are often stocked in reservoirs in conjunction with other predators such as hybrid striped bass or striped bass (Schultz and Dodd 2008). The impetus for stocking both species is to take advantage of surplus forage such as Gizzard Shad and provide additional angling opportunities (Heidinger 1999). However, this could be counter-productive if the two species compete for the same resource, resulting in increased natural mortality. While Walleye and hybrid striped bass forage on gizzard shad, Walleye can have a gape limitation preventing them from foraging on adult Gizzard Shad resulting in a bottleneck (Einfalt and Wahl 1997). For example, Ward et al. (2007) found an absence of adult Gizzard Shad in a Walleye consumption analysis and concluded that only age-0 Gizzard Shad were available to Walleye. In contrast, Striped Bass can consume clupieds up to 60% of their total length (Manooch 1973). It is assumed the relationship between consumption of clupeids based on length by hybrid striped bass is similar to Striped Bass, based on their morphological similarities. Thus, Walleye can be at a disadvantage if they are competing with hybrid striped bass for Gizzard Shad, given their narrow ability to forage on all prey sizes.

There is abundant evidence to suggest Walleye and moronid species experience competition with each other (Forney 1977; Neal et al. 1999; Patrick and Moser 2001; Raborn et al. 2002; Raborn et al. 2004; DeBoer et al. 2013). However, competition is difficult to identify as it requires resources to be limited and the competing species must have a significant niche overlap (Wiens 1993). Further, stocking abundance of hybrid striped bass negatively influence recruitment of Walleye in Monroe Reservoir (Doll 2015), suggesting competition is occurring between these two species that could influence natural mortality.

While natural mortality is generally out of the control of the manager when it is due to abiotic factors (e.g., temperature), when natural mortality results from competitive forces the manager can indirectly take steps to mitigate its effect. Evidence suggests age-0 Walleye recruitment to the fall season is negatively related to stocking abundance of hybrid striped bass (Doll 2015). While this interaction occurs before recruitment to the sport fishery, it is assumed the mechanisms causing the negative response are from competition. Therefore, conditional natural mortality could be varying annually with concurrent stockings of hybrid striped bass. In years with high stocking abundance of hybrid striped bass, conditional natural mortality of Walleye could be more similar to the high end (cm = 0.50) used in our simulations. In contrast, during years of moderate to low stocking of hybrid striped bass, conditional natural mortality of Walleye is likely more similar to the moderate (cm = 0.30) to low (cm = 0.20) end. Thus, expected yield could be influenced by stocking abundance of these two species. More information is needed to more accurately estimate current conditional natural mortality and fishing mortality, particularly considering the known niche overlap between Walleye and moronids (Neal et al. 1999; Patrick and Moser 2001; Raborn et al. 2002; Raborn et al. 2004; DeBoer et al. 2013).

Habitat requirements are an unmeasured variable that could influence hybrid striped bass natural mortality. While limited information is available on specific habitat requirements for hybrid striped bass, there is substantial work on the habitat requirements of Striped Bass. For example, the dissolved oxygen-temperature squeeze hypothesis of Counant (1985 and 2013) has been widely accepted for Striped Bass. This hypothesis states that adult Striped Bass require cool (< 25°C) and oxygenated (> 2 mg/L) water to survive. It is unclear if the same hypothesis applies to hybrid striped bass considering they are thought to tolerate warmer temperatures (Coutant 2013). Natural mortality could be increased if this habitat requirement is limiting and thus influence our estimates of potential yield. At Monroe Reservoir optimal habitat based on dissolved oxygen and temperature has been estimated at only 22% of the lake volume during summer (Hoffman et al. 2013). This suggests that density dependent mechanisms could be influencing hybrid striped bass natural mortality if the dissolved oxygen-temperature squeeze hypothesis is applicable.

Our study populations have many similarities to other Midwestern reservoirs, suggesting the posterior distribution of model parameters we generated using Bayesian analysis could be incorporated in other studies as prior information. For example, Walleye growth and mortality parameters were consistent with other exploited populations across the U.S. (Quist et al. 2003; Quist et al. 2004). Similarly, our hybrid striped bass growth parameter estimates were consistent with those reported for other Midwestern lakes (Schultz et al. 2013). However, there is limited research that documents mortality of hybrid striped bass. Nevertheless, our estimates of total annual mortality (M = 0.31) is similar to what was reported by Schultz and Dodd (2008) in an Iowa lake (M = 0.36). Thus, if managers are seeking to describe yield and has limited

information on growth or mortality our results could be used as prior information that will permit the generation of improved estimates for yield-per-recruit model inputs.

There is limited application of yield-per-recruit models to guide management of Walleye and moronid species (Schultz and Dodd 2008; Hoffman et al. 2013). Schultz and Dodd (2008) studied Walleye and hybrid striped bass yield-per-recruit models and suggested that natural mortality was most important in determining fishing quality in an urban Iowa reservoir and thus no management action was necessary. However, their study only evaluated exploitation rates less than 0.30 and did not observe yield to reach a maximum. We evaluated higher exploitation rates and observed yield to reach a maximum at exploitation rates as low as 0.25 for Walleye and 0.30 for hybrid striped bass, suggesting fishing mortality is important in determining the fishing quality. Hoffman et al. (2013) also suggested that current management of hybrid striped bass in Monroe Reservoir was adequate to maintain the fishery. However, Hoffman et al. (2013) used one year of data and point estimates for model parameters to estimate yield. Our study improves upon that of Hoffman et al. (2013) by incorporating multiple years of data and uncertainty in our yield estimates. By incorporating multiple years of data, we found that growth overfishing was not occurring at minimum size limits greater than 250 mm, while it was found with the Hoffman et al. (2013) study.

The current minimum length limits in our study population (356 mm for Walleye and no minimum length limit for hybrid striped bass) were not maximizing yield, and growth overfishing is expected under certain scenarios. At these length limits and calculated natural mortality, the yield isopleths suggested maximum yield would be obtained by increasing the minimum length limit of both species if exploitation was moderate to high. However, if exploitation was low, no change in yield would be expected with an increase in the minimum

size limit. Increases in yield have been observed in Walleye populations over a three year period following an imposition of a minimum size limit in other impoundments (Stone and Lott 2002). For example, in a Missouri River impoundment, the Walleye population was declining until a minimum size limit of 356 mm was imposed, increasing yield four-fold in three years (Stone and Lott 2002). Additional information on exploitation will allow the model to generate specific predictions based on the current conditions.

Management Implications

Minimum size limits and bag limits are directly controlled by the fisheries manager and evaluated with the yield-per-recruit model. While minimum length limits are generally imposed to protect spawning individuals in a self-sustaining population (Brousseau and Armstrong 1987), our study populations are maintained through annual stocking and natural recruitment is thought to be insignificant (Dave Kittaka, personal communication). Thus, minimum size limits are manipulated to maximize harvest before the fish succumb to natural mortality. Given additional information about exploitation, the results of this research can be used to direct decision making with regards to the minimum size limits with knowledge about the uncertainty in estimated yield.

Exploitation rate can be modified by changing the bag limit. However, without knowing the current level of exploitation this piece is difficult to justify changing. Thus, it is of great importance that exploitation rate be identified when using yield-per-recruit models to evaluate yield. The exploitation rate could be identified with a tagging study in conjunction with a creel survey. Specifically, fish should be marked with tags and released into the population in the early spring. The following creel survey would monitor harvested fish and the proportion of

individuals harvested with tags can be used to extrapolate to an estimate of exploitation. A number of individuals should also be double tagged to estimate tag loss.

An additional management action that could influence yield is stocking abundance of competitors. While natural mortality cannot be directly influenced by the manager, it can be manipulated indirectly if competition exists between two stocked species. That is, by increasing or decreasing stocking abundance of competitors the manager can influence natural mortality of both stocked species. To determine the extent of competition and identify food web dynamics, stomach content analysis or isotope analysis should be conducted.

Additional management goals to consider are the number and size of harvested fish. In some cases the yield-per-recruit model predicts maximum yield to be similar across minimum size limits. However, there is a tradeoff of number and size. Typically a smaller size limit will result in the harvested fish being dominated by smaller fish but in greater numbers in contrast to a higher size limit that would result in the harvested fish being dominated by larger fish but fewer numbers. Recommendations for management based on expected yield of both species evaluated during this research requires two additional pieces of information: 1) Exploitation rate needs to be estimated and 2) a more accurate estimate of natural and fishing mortality needs to be assessed. While assumptions can be made to provide management decisions now, this information would increase the certainty in the recommendations above.

Chapter 4: Estimating Capture Probabilities While Accounting for Schooling Behavior of Common Stream Fish

Abstract: Estimating abundance of organisms is one of the fundamental state variables ecologists seek to describe. However, organisms are often imperfectly detected. Imperfect detection is defined as the realization that not all organisms are observed when they are present. Imperfect detection leads to biased estimates of abundance and assemblage level descriptors. Schooling behavior, such as schooling in fishes increases this bias, which confounds the efficacy of traditional models in estimating abundance and capture probability. Although multi-pass depletion sampling of fish can be used to account for some of the bias, assuming fish behave independently, quantifying this behavior is required to fully understand fish abundance. Our objective was to extend the multinomial model of Royle (2004) and Dorazio et al. (2005) to account for schooling behavior and determine capture probabilities of common stream fishes in wadeable streams of the Eastern Corn Belt Plain of Indiana. The multinomial and extended models were evaluated with both empirical and simulated data. A total of 12,009 fish representing 65 species and 1 hybrid were sampled during the project. Estimated capture probabilities of stream fishes were consistently lower when schooling behavior was ignored. We observed a maximum of 70% increase in capture probabilities and an average increase of 16% when accounting for schooling behavior. Capture probabilities that are underestimated can result in significantly higher estimates of abundance, thus concluding there are more individuals present. Our estimated capture probabilities can be applied to standard electrofishing surveys to improve the accuracy of abundance estimates and can be applied to biological monitoring tools

to create multimetric indices that are more sensitive to perturbation. Finally, our model can be applied to surveys of any species where a multi-pass removal survey is conducted.

Key words: detectability, beta-multinomial, Bayesian, hierarchical model, community assessment

INTRODUCTION

Estimating abundance of organisms is one of the fundamental state variables ecologists seek to describe. Abundance metrics are often described as species abundance distribution patterns (Preston 1948), diversity indices such as Simpson's D, multivariate analysis methods (McCune and Grace 2002), or multimetric indices (Karr 1981). These values are typically acquired through common sampling protocols that result in a relative index of abundance which is a product of the observed number of individuals and an unknown and unmeasured term, detectability (Royle and Dorazio 2008). Thus, the estimated abundance (n) is a product of the true number of individuals occupying a site (N), and the capture probability (p): $n = pN$. Capture probability is defined as the probability of capturing an individual given that it is present. Because capture probabilities vary with methods, habitats, environments, etc. (Korman et al. 2009; Hense et al. 2010; Dextrase et al. 2014), the percentage of individuals that are detected may or may not represent the true abundance, particularly when comparisons are across sites and include multiple species.

Imperfect detection occurs when the observed organisms does not include all individuals present. While it is common for organisms to be undetected, it is sometimes necessary to acknowledge this limitation to determine the true abundance of organisms. Accounting for imperfect detection has become conventional practice (Kéry et al. 2009; Weir et al 2009; King et al. 2011; Regan et al. 2011; Zuckerberg et al. 2011; Chen et al. 2013; Pfaller et al. 2013; Dextrase et al. 2014; Papadatou et al. 2012; Péron et al. 2014), yet, it remains a topic of debate (Welsh et al. 2013; Banks-Leite et al. 2014; Guillera-Arroita et al. 2014). While accounting for imperfect detection may provide little benefit under some circumstances (e.g., high heterogeneity in occupancy, Welsh et al. 2013), models that account for imperfect detection provide improved

estimators (MacKenzie et al. 2002; Tyre et al. 2003; Guillera-Arroita et al. 2014). In contrast, others have suggested designing experiments that control covariates of capture probability can yield qualitatively similar results between estimates adjusted for imperfect detection and those that are not (Banks-Leite et al. 2014). However, intrinsic behavior in organisms is a covariate that cannot be controlled. Thus, while it is not always suggested, accounting for imperfect detection is often required. Statistical methods that permit accounting for imperfect detection can improve our understanding of the true abundance and distribution of organisms.

Unknown and unmeasured variables can influence the observation process. This limitation can result in difficulty in detecting meaningful long-term abundance trends (Kéry et al. 2005) or changes in community structure (MacKenzie et al. 2004). For example, if the true abundance of species A and B sums to 100 at a site, and the capture probability of species A is 75% (i.e., we observe 75% of the total number of individuals at a site) and the capture probability of species B is 25%. Thus, we observe 75 individuals of species A and 25 of species B. Next, each population increased by a factor of two, and our following survey resulted in observation of 150 individuals of species A and 50 of species B. Assuming equal detectability, we would conclude there was a greater increase in abundance of species A compared to species B. However, the true abundances increased equally for both. Further, we also might incorrectly conclude that species A comprises a larger portion of the community than species B when in fact they are equal. While this is a simple theoretical example, the implications of imperfect detection on species distribution (Kéry and Schmidt 2008) and abundance estimates (Kéry et al. 2005) are vast.

Imperfect detection (and subsequent estimates of abundance) can be most problematic in community assessments when study goals include some measure of abundance. Multimetric

indices, such as the Index of Biotic Integrity (IBI; Karr 1981) have been used to assess the health of streams for decades (Karr 1981; Simon and Dufour 1997; Barker et al. 2006; Qadir and Malik 2008; Kido 2013). Unfortunately, the sensitivity in detecting shifts in fish assemblages using an IBI is restricted to major perturbations (Trebitz et al. 2003). Improvements in describing stream health and improving sensitivity are possible using other methods, such as multivariate analysis (Thomas & Hall 2006), but typically require different or more extensive data. One such factor limiting sensitivity in the IBI is our ability to obtain accurate estimates of fish abundance, as capture probability is influenced by individual fish behavior (Martin et al. 2011). By refining something this basic with respect to capture (e.g., reduced variability and increased accuracy), we can advance our ability to detail stream health, regardless of the multimetric method employed in the analysis.

Inaccurate estimates of the true abundance or presence of an organism can be problematic (Archaux et al. 2011; Lahoz-Monfort et al. 2013). The additional noise from detecting individuals imperfectly can result in increased type II error, ultimately exasperating our abilities to detect ecologically important differences (Archaux et al. 2011). Substantial progress has been made designing sampling protocols and statistical models to estimate and account for capture probability (Bayley and Peterson 2001; Kéry 2002; MacKenzie et al. 2002; Royle and Nichols 2003; Royle 2004; Mäntyniemi et al. 2005). Yet, with few exceptions (e.g., Martin et al. 2011) these models assume organisms are detected independently from each other (Royle and Dorazio 2008). Behavior such as schooling can violate this assumption. Schooling behavior can impose a correlated response among individuals where observing one individual increases the probability of observing another individual, resulting in a biased estimate of detectability and the resulting estimate of abundance.

One method to estimate capture probability of stream fishes is a multiple pass survey design in a closed system (Zippin 1956; Otis et al. 1978), with the results modeled as a multinomial response (Dorazio et al. 2005). Unfortunately, this model does not account for the schooling behavior of fishes. Therefore, our objective was to extend the multinomial model of Royle (2004) and Dorazio et al. (2005) to account for schooling behavior and determine capture probabilities of common stream fishes in wadeable streams of the Eastern Corn Belt Plain of Indiana. The multinomial and extended models were evaluated with both empirical and simulated data. We hypothesized that accounting for schooling behavior in the extended model will result in more accurate and precise estimates of capture probabilities.

METHODS

Site description and data collection

Fifteen sites with a drainage area of less than 2,600 km^2 were randomly selected from the Indiana Department of Environmental Management's sampling site list for their probabilistic monitoring program in the Eastern Corn Belt Plain Ecoregion (Figure 17). Sampling was conducted between June 19 and August 8, 2013 with a four person crew. The crew was consistent during the entire project. Each site was closed off with a block net placed at the upstream and downstream ends to restrict fish movement during the survey. The distance sampled at each site was set at 15 times the wetted width. Three passes with a tote-barge DC electrofishing unit were conducted in an upstream pattern. At the end of each pass, fishes were identified to species, counted, and held in large tanks until the survey was completed. Species that required visual examination under a dissecting microscope were preserved in formalin on

site and transported to Ball State University. Methodology was approved by the Ball State University Animal Care and Use Committee (IACUC Protocol #:317058-1).

Modeling approach

We estimated and compared capture probabilities using two models. The first was the multinomial model of Royle (2004) where the detection process is assumed to follow a normal distribution on the logit scale. Thus, schooling behavior is not accounted for. Our second model extended the Royle (2004) model to account for schooling behavior. To accomplish this, we adopted an approach used by Martin et al. (2011) and Dorazio et al. (2005). Martin et al. (2011) extended the N-mixture model of Royle & Dorazio (2008) to account for correlated behavior (e.g., schooling) by assuming the probability parameter in the binomial distribution followed a beta distribution. Dorazio et al. (2005) extended the Royle (2004) multinomial model using the beta distribution to describe detection; however, their model had an additional hierarchical connection between abundance at each site. Here, we were interested in describing capture probability across a landscape where individual site detection was related in a hierarchical framework, but abundances were not. Specifically, our hierarchical structure on capture probability was at the family level and detection probability of each species within a family was assumed to come from a common distribution. Therefore, to account for correlated behavior we modeled the detection process with a beta distribution, hereafter referred to as the beta-multinomial model.

Model description - multinomial model

The first model does not account for correlated behavior and is referred to as the multinomial model (Royle 2004). This model requires data to be collected under a removal protocol where samples are taken from each site *i* which is considered a spatially distinct subpopulation. We assume that the subpopulation is closed and there are no changes in births, deaths, immigration, or emigration during the removal survey at individual sites. Due to the spatial differences among our sites, it is also assumed that individuals are not permitted to move between subpopulations. Thus, abundance at each site is considered independent.

This sampling protocol yields the number of fish observed x_{ij} in the j^{th} removal (for $j = 1,\ldots J_i$) at site *i*. The observations are modeled as a multinomial outcome:

$$\text{Equation 1:} \quad [x_{i1}, x_{i2}, x_{i3}, \ldots x_{iJ_i} | N_i, \boldsymbol{p}] \sim \text{Multinomial}(N_i, \boldsymbol{p})$$

Where N_i is the unknown number of fish at site *i* and **p** is the probabilities of capture associated with the J_i removals. Thus, p_{ij} is the capture probability during the j^{th} removal at the i^{th} site. Abundance N_i is modeled using an N-mixture model with Poisson distribution.

$$\text{Equation 2:} \quad N_i \sim \text{Binomial}(pcap_i, n_i)$$

$$\text{Equation 3:} \quad n_i \sim \text{Poisson}(\lambda_i)$$

$$\text{Equation 4:} \quad pcap_i = \sum_{j=1}^{J_i} p_{ij}$$

Where n_i is the latent unknown true number of fish at site *i* that is modeled with a Poisson distribution, λ_i is the Poisson mean abundance at site *i*, and $pcap_i$ is the total capture probability at site *i*. Variability in abundance could be modeled here as a linear covariate of effects using the log link on λ_i.

Letting π_i denote the probability of capture during a single removal at site *i*, individual removal capture probabilities, p_{ij}, are calculated as:

$$\text{Equation 5:} \quad p_{ij} = \pi_i (1 - \pi_i)^{j-1}$$

We assume π_i is constant for site i. In the multinomial model π_i is considered an independent coefficient estimated from the data. Covariates of capture probabilities could be modeled here using the logit link. Without covariates, π_i is modeled with a normal distribution with the logit link.

Equation 6: $\text{logit}(\pi_i) \sim \text{Normal}(0, 0.001)$

Model description - beta-multinomial model

The second model, beta-multinomial model, is an extension of the multinomial model where π_i follows a beta distribution. Here, equations 1 through 5 are not changed while equation 6 is replaced by equations 7 through 10. Thus, π_i is modeled with a beta distribution having parameters p_i and q_i which are parameterized in terms of its mean and variance following Cepeda-Cuervo (2015).

Equation 7: $\pi_i \sim \text{Beta}(p_i, q_i)$

Equation 8: $p_i = \mu_i * \phi_i$

Equation 9: $q_i = \phi_i - (\mu_i * \phi_i)$

Where p_i and q_i are the shape and rate parameters of the beta distribution for site i, μ_i is the mean, and ϕ_i is interpreted as the precision parameter (see Cepeda-Cuervo 2015, for more details). From here, μ_i can be modeled as a linear function of covariates using the logit link to investigate the influence of parameters on capture probability. Without covariates, μ_i is modeled with a normal distribution with the logit link.

Equation 10: $\text{logit}(\mu_i) \sim \text{Normal}(0, 0.001)$

Model assumptions

The multinomial model assumes the population is closed to immigration and emigration during the survey. Individuals are only counted once and after each pass they are removed from the population and cannot be counted again. The model also assumes capture effort is constant for each pass within each site and the capture probability is constant for all individuals in the population. Finally, the multinomial model also assumes individual behave independently of each other.

The beta-multinomial model retains all assumptions except independent behavior of individuals. The beta distribution allows for over-dispersion in the capture probabilities, meaning capture probabilities are permitted to be higher or lower than would be expected with the multinomial model. Thus, schooling behavior (e.g., schooling or congregating around preferred habitat) that would induce correlation among observations is accounted for.

Model application – empirical data

Parameters were estimated for each species as a hierarchical model on capture probability. We assumed phylogenetic relationships between species of the same family could inform capture probabilities of species with limited data, thus species was treated as a random effect so that the capture probability parameters for each species were assumed to come from a global distribution by family. The parameters π_i of the multinomial model and μ_i of the beta-multinomial model were logit transformed and given a normally distributed non-informative hierarchical prior for each family. The capture probability coefficients (π_i and μ_i) of the model are interpreted as a percent capture.

Model validation – simulated data

We tested the accuracy and precision of our modeling framework with simulated data. Three pass depletion data for three species of the same family at ten sites were simulated under the assumption that species school, thus resulting in the true detectability following a beta distribution (Appendix B-3). Accuracy in detectability estimates using the standard multinomial model and our beta-multinomial model was assessed using the relative bias $\hat{B}_{ij}$ for species *i* and site *j* (Equation 11).

$$\text{Equation 11:} \quad \hat{B}_{ij} = \frac{\hat{p}_{ij} - p_{ij}}{p_{ij}}$$

Where $\hat{p}_{ij}$ is the capture probability estimate for species *i* and site *j*, and p_{ij} is the "true" capture probability used for the simulated species *i* and site *j*. When $\hat{B}_{ij} > 0$, the estimator is positively biased and thus overestimates capture probabilities. Overestimation of capture probabilities will result in underestimation of abundance. Conversely, when $\hat{B}_{ij} < 0$, the estimator is negatively biased and thus underestimates capture probabilities. Similarly, underestimation of capture probabilities will result in overestimation of abundance. We report median and 95% credible intervals for the estimates of relative bias.

Bayesian inference

All models were fit using Bayesian inference in R 3.1.1 (R Core Team 2014) using JAGS 3.4 (Plummer 2003) and rjags 3.13 (Plummer 2014) in a cluster computing system. All parameters were given non-informative priors. Three concurrent MCMC chains were run discarding 100,000 steps, thinning 100 steps, and saving 500,000 steps. All parameters were given non-informative priors. Convergence of the MCMC chains were checked using the Brooks-Gelman-Rubin (BGR) scale-reduction factor (Brooks and Gelman 1998). The BGR factor is the ratio of between-chain variability to within-chain variability. The chains have

converged when the upper limits of the BGR factor are close to one. Values less than 1.15 suggests the MCMC chains have converged. Posterior distribution of the parameter estimates are describe with their median and 95% credible interval. Complete model specification of the multinomial and beta-multinomial model using JAGS code can be found in the Appendix (Appendix B).

Due to the complexity of the model and large dataset we used the cluster computer system available at Ball State University. The Ball State University cluster consists of 32 Dell PowerEdge R420's with dual 2.6 GHz 8 core Xeon ES-2670 processor and 62 GB RAM and 450 GB of local disk storage. Total cluster shared storage is 9 TB in a raid 5 array hosted on the head node. All nodes are connected at 1GBs with an HP Procurve 5300xl switch.

RESULTS

A total of 12,007 fish representing 64 species and 1 hybrid (13 families) was sampled during the project (Appendix C). Species richness at individual sites ranged from 18 to 37 species. The sites with highest richness were Wildcat Creek (37 species), Whitewater River (32 species), and Nolan's Fork (29 species).

Multinomial model – Empirical data

The multinomial model converged and estimated capture probabilities for five families (57 species and 1 hybrid). The sample size of the remaining families prevented the model to converge at a posterior distribution. Estimated capture probability for Catostomidae was 0.37 (Figure 18; 95% CI = 0.25 to 0.45). Cyprinidae capture probabilities were 0.34 (Figure 18; 95% CI = 0.28 to 0.40). Centrarchidae and Percidae capture probabilities were 0.20 (95% CI = 0.03 to

0.38) and 0.19 (Figure 18; 95% CI = 0.08 to 0.27). Ictaluridae had the lowest capture probability (Figure 18; 0.002, 95% CE = $6.1*10^{-5}$ to 0.09). Capture probabilities were only different between Cyprinidae and Percidae based on non-overlapping 95% CI (Figure 18).

Catostomidae capture probabilities across species were consistent, with median values ranging from 0.36 to 0.38 (Figure 19-A). Uncertainty (i.e., width of 95% CI) in estimates for Golden Redhorse *Moxostoma erythrurum*, Northern Hogsucker *Hypentelium nigricans*, and White Sucker *Catostomus commersonii* ranged between 0.14 and 0.15. Quillback Carpsucker *Carpiodes cyprinus* and Shorthead Redhorse *Moxostoma macrolepidotum* capture probabilities were the most uncertain with 95% CI widths of 0.36 and 0.41 (Figure 19-A).

Capture probabilities of Cyprinidae species were variable with median estimates ranging from 0.25 (Bluntnose Minnow *Pimephales notatus*) to 0.43 (Central Stoneroller *Campostoma anomalum*; Figure 20-A). However, 95% credible intervals of 20 out of 22 species overlapped each other indicating no credible difference among capture probabilities.

Median capture probabilities for individual Centrarchidae species ranged from 0.09 (Largemouth Bass *Micropterus salmoides*) to 0.73 (Pumpkinseed Sunfish *Lepomis gibbosus*; Figure 21-A). The low capture probability for Largemouth Bass is similar to a closely related species, the Smallmouth Bass *Micropterus dolomieu* (0.11). Capture probabilities for the remaining species ranged from 0.12 to 0.37 (Figure 21-A).

Percidae capture probabilities were consistent among species (Figure 22-A). Median Percidae capture probabilities ranged from 0.15 (Orangethroat Darter *Etheostoma spectabile*) to 0.25 (Johnny Darter *Etheostoma nigrum*). Upper credible intervals for all Percidae species were less than 0.50 (Figure 22-A), indicating there is less than a 50% probability of capturing a darter if it is present.

Ictaluridae capture probabilities were also consistent among species (Figure 23-A). Upper credible intervals for all Ictaluridae species were below 0.15 (Figure 23-A). However, the posterior distribution of capture probabilities for all Ictaluridae species was skewed towards 0 (Figure 23-A).

Beta-multinomial model – Empirical data

Fifty seven species and one hybrid from five families were included in the beta-multinomial model. The sample size of the remaining families prevented the model to converge at a posterior distribution. Median estimated capture probability for Catostomidae was 0.43 (Figure 24; 95% CI = 0.27 to 0.54), while Cyprinidae capture probability was 0.39 (Figure 24; 95% CI = 0.33 to 0.45). Centrarchidae and Percidae median capture probability was 0.33 (95% CI = 0.08 to 0.43) and 0.20 (Figure 24; 95% CI = 0.04 to 0.30). Ictaluridae had the lowest capture probability (Figure 24; 0.001, 95% CE = $5.3*10^{-5}$ to 0.24). Capture probabilities were only different between Cyprinidae and Percidae based on non-overlapping 95% CI (Figure 24).

Catostomidae capture probabilities estimated with the beta-multinomial model across species were similar with median values ranging from 0.43 to 0.44 (Figure 19-B). Uncertainty (i.e., width of 95% CI) in estimates for Golden Redhorse, Northern Hogsucker, and White Sucker were 0.22 to 0.24. Quillback Carpsuckers, River Redhorse *Moxostoma carinatum*, Shorthead Redhorse, and Silver Redhorse *Moxostoma anisurum* capture probabilities were the most uncertain with 95% CI widths of 0.42 (Figure 19-B).

Capture probabilities of Cyprinidae species were similar among species with median estimates ranging from 0.38 (Bluntnose Minnow) to 0.41 (Central Stoneroller; Figure 20-B).

Further, 95% credible intervals of all species overlapped each other indicating no credible difference among capture probabilities.

Median capture probabilities for individual Centrarchidae species ranged from 0.29 (Largemouth Bass) to 0.41 (Longear Sunfish *Lepomis megalotis*; Figure 21-B). Capture probabilities were most uncertain for Pumpkinseed Sunfish (95% CI = 0.6 to 0.81) while Longear Sunfish estimates were the most precise (95% CI = 0.30 to 0.49).

Percidae capture probabilities were consistent among species (Figure 22-B). Median Percidae capture probabilities ranged from 0.18 (Orangethroat Darter) to 0.22 (Greenside Darter *Etheostoma blennioides*). Upper credible intervals of capture probabilities for all Percidae species were less than 0.40 (Figure 22-B).

Ictaluridae capture probabilities were also consistent among species (Figure 23-B). Upper credible intervals for Flathead Catfish *Pylodictis olivaris* were 0.27 and 0.16 for Brindled Madtom *Noturus miurus*. However, the posterior distribution of capture probabilities for all Ictaluridae species was skewed towards 0 (Figure 23-B).

Model comparison – Empirical data

Capture probabilities from both models were estimated for five families (Figure 18 and 24). The remaining families were only represented by single species or sampled infrequently and capture probabilities could not be reliably estimated (e.g., Clupeidae, Cottidae, Esocidae, Petromyzontidae, Poeciliidae, Salmonidae, and Sciaenidae; Figure 18 and 24).Capture probabilities with the beta-multinomial model were 18% (Catostomidae), 68%, (Centrarchidae), 15% (Cyprinidae), and 2% (Percidae) higher than those estimated with the multinomial model (Figures 18 and 24). In contrast, capture probabilities for Ictaluridae decreased 43%. However,

the median capture probability for Ictaluridae for both models remained below 1% (Figure 18 and 24).

Most individual species had higher capture probabilities with the beta-multinomial model compared to the multinomial model. Capture probabilities of individual Catastomidae species increased at a similar rate from the multinomial to beta-multinomial species, ranging from 15% (Golden Redhorse) to 21% (White Sucker) (Figure 19). Capture probabilities of two Cyprinidae species decreased with the beta-multinomial model while the others increased (Figure 20). While most Centrarchidae species exhibited an increase in capture probabilities with the beta-multinomial model compared to the multinomial model, the median of the posterior distribution for Pumpkinseed sunfish decreased 51% from 0.73 (multinomial model) to 0.36 (beta-multinomial model) (Figure 21). Capture probabilities of one Percidae species (Johnny Darter) decreased from 25% (multinomial model) to 21% (beta-multinomial model). The remaining Percidae species increased when accounting for schooling behavior (Figure 22). Individual Ictaluridae species decreased when accounting for schooling behavior. However, the posterior distribution of capture probabilities for all Ictaluridae species was skewed towards 0 (Figure 23-B).

Multinomial model – Simulated data

Median estimates of capture probabilities estimated using the multinomial model with simulated data ranged from 0.38 to 0.59 and averaged 0.49, compared to the true capture probabilities ranging from 0.08 to 0.87 and averaged 0.42 (Figure 25). A linear trend did not exist between the true capture probabilities and those estimated with the multinomial model (Figure 25). Median estimates of relative bias in capture probabilities using the multinomial

model ranged from -0.57 to 9.03 and averaged 1.34 (Figure 26-A1, A2, and A3). This indicated the average estimated capture probability was 134% greater (or more than twice) than the true capture probability. Uncertainty in relative bias (i.e., width of 95% CI) for species specific capture probabilities of the three species averaged 2.4, 0.6, and 0.5 (Figure 26-A1, A2, and A3). Ten of the 30 species/site combinations resulted in the relative bias 95% CI to overlap 0, including eight sites with species 1 (Figure 26-A1) and two sites with species 3 (Figure 26-A3). This suggested that 30% of the estimates are not credibly different from the true capture probabilities.

Beta-multinomial model – Simulated data

Median estimates of capture probabilities estimated using the beta-multinomial model ranged from 0.01 to 0.84 and averaged 0.39 (Figure 25). In contrast to the multinomial model, there was a linear trend between the true capture probabilities and capture probabilities estimated with the beta-multinomial model (Figure 25). Median estimates of relative bias in capture probabilities ranged from -1.00 to 5.35 and averaged 0.13 (Figure 26-B1, B2, and B3). This indicated that the averaged estimated capture probability is 13% greater than the true capture probability. Uncertainty in the relative bias (i.e., width of 95% CI) for species specific capture probabilities of the three species averaged 1.9, 2.6, and 2.2 (Figure 26-B1, B2, and B3). All of the species/site combinations resulted in the relative bias 95% CI that overlapped 0. This suggested that all of the estimates are not credibly different from the true capture probability.

Model comparison – Simulated data

Two differences were observed between the multinomial and beta-multinomial model results using the simulated data. First, the multinomial model was more precise based on the widths of the credible intervals (average 1.1) and second, the multinomial model was less accurate based on 43% of the credible interval estimates for the relative bias overlapping zero.

DISCUSSION

Our study extended the multinomial model of Royle (2004) and Dorazio (2005) to account for schooling behavior and we compared capture probability estimates between our beta-multinomial model and the multinomial model using an empirical and simulated dataset. This allowed us to verify that including schooling behavior in the model provided higher probability of capture estimates. Estimated capture probabilities from the empirical data using the multinomial model were generally lower than those estimated from the beta-multinomial model, and species specific capture probabilities were closer to the overall family mean with the beta-multinomial model. Finally, analysis of simulated data indicated that capture probabilities estimated with the beta-multinomial model were more accurate but less precise than with the multinomial model.

The depletion sampling protocol that is used to estimate abundance and capture probabilities has a long history of use in ecology (Otis et al. 1978; Raleigh and Short 1981; Riley and Fausch 1992; Jung et al. 2005; Odenkirk and Smith 2005; Hense 2010), but has not been expanded to account for schooling behavior in a hierarchical framework. The most popular and simplest model to estimate abundance and capture probabilities was described by Zippin (1956). Assumptions of this model include a closed population, constant capture effort, and capture probability is constant for all individuals in the population. Other more novel methods of

estimating abundance and capture probabilities have been developed to relax some of the assumptions of the Zippin model (Wyatt 2002; Mäntyniemi et al. 2005; Dorazio et al. 2005). Our beta-multinomial model expands this suite of imperfect detection models applied to depletion sampling data by accounting for correlated behavior that result in individuals being aggregated.

Schooling behavior has been accounted for in some imperfect detection models (Mäntyniemi and Romakkaniemi 2002; Martin et al. 2011); however, ours is the first using a multinomial model that includes family level relationships. Correlated behavior that is shared by individuals of the same family can be induced by schooling and schooling near preferred habitat, such as, schooling of salmonid smolt during their migration (Hartman et al. 1967) and microhabitat selection by the Rosyside Dace *Clinostomus funduloides*, Creek Chub *Semotilus atromaculatus*, and Warpaint Shiner *Luxilus coccogenis* in lotic systems (Grossman and Freeman 1987).

Our hierarchical linkage on capture probability at the family level is based upon the idea that phylogenetic relationships induce correlation of traits among closely related species. Phylogenetic relationships need to be included when testing ecological mechanisms (Felsenstein 1985; Gotelli and Pyron 1991; Ackerly and Reich 1999; LeRoy Poff et al. 2006; Kraft et al. 2007; Willis et al. 2008). By acknowledging that observed variation is due to species evolutionary relationships has gleaned new insights (Gillespie 2004) and refuted others (Jacquemin and Doll 2014).

Schooling behavior present in our empirical data influenced capture probabilities; however, the affect was not consistent across families or sites suggesting the degree of schooling behavior can result in a different impact on the probability of capture. Based on our analysis of empirical data, capture probabilities were consistently lower when we ignored schooling

behavior but varied in how much lower. For example, Centrarchidae capture probabilities increased the most when we accounted for schooling behavior while Cyprinidae did not exhibit the same magnitude of increase. Martin et al. (2011) showed that just a moderate level of correlation can result in substantial underestimation of capture probability, thus any behavioral activity that could potentially induce a correlated response can impact capture probability and subsequent abundance estimates. While Cyprinidae species are generally considered schooling organisms, adult Centrarchidae species are not, suggesting schooling behavior of Centrarchidae may bias models that ignore this behavior more than we predicted. Underestimated capture probabilities result in significantly higher abundance estimates. Given this (incorrect) scenario, we would conclude there were more fish in a stream than actually present.

Our beta-multinomial model is the first that is parameterized with a hierarchical relationship at the family level which allows us to make generalizations at multiple levels. Typical approaches to applying a hierarchical framework with imperfect detection models assume a metapopulation distribution and behavior, where abundance is treated as the exchangeable parameter (Royle and Link 2005; Dorazio et al. 2005; MacKenzie et al. 2009) and inference for abundance is at the site and population level. Our exchangeable parameter was capture probability and linked at the family level so that we can draw conclusions about detectability of individual species and families. However, Gotelli and Taylor (1999) showed that stream fishes extinction and colonization patterns do not fit a metapopulation model.

The hierarchical structure of our beta-multinomial model also permits our results to be used as Bayesian prior distributions in other studies. Our estimates of capture probabilities can be applied to new studies as an informative prior for species in the families we examined. For example, Golden Shiner *Notemigonus crysoleucas* was not sampled in our study but occurs

throughout much of the United States (Jenkings and Burkhead 1993) including our study area. In the absence of other information, researchers could use our estimate of Cyprinidae capture probability as a Bayesian informative prior for Golden Shiner and calculate more accurate abundance estimates from, for example, a tote barge electrofishing survey.

The beta-multinomial model improved accuracy in estimated capture probability with reduced precision in the relative bias estimate. The uncertainty in our capture probability estimates using simulated data with the beta-multinomial model always overlapped the true value, a result we did not observe with the multinomial model. Ideally, a model will have the highest accuracy and precision, however, this is often not attained in ecological models (Hellmann and Fowler 1999). However some authors argue an estimator that is more accurate but less precise is preferred over one that is less accurate but more precise (Bolker 2008). Thus we believe our beta-multinomial model is an improvement over the multinomial model by providing a more accurate estimate of capture probability (and thus abundance) at the cost of precision.

Our model can be extended or modified to account for a variety of scenarios and conditions that could impact abundance and detection. For example, we assumed abundance was described by a Poisson distribution. If overdispersion in abundance is present (mean and variance are not equal), abundance could be modeled as a negative binomial distribution. If overdispersion is present and not accounted for by using the negative binomial model, the estimated variance would be biased. Additionally, we formulated the detectability model (Equation 7-10) so that it can easily incorporate covariates of capture probability using the beta regression approach of Cepeda-Cuervo (2015). The influence of additive effects on capture probability can be evaluated using the logit link on the μ_i parameter. This allows researchers to

easily apply our model to answer a variety of questions regarding what covariates influence detection wile accounting for schooling behavior.

We believe our model is useful to both ecological managers and modelers by accounting for aggregative behavior in a population model that can be applied to a variety of species and also provides more accurate estimates of capture probabilities. Additionally, the improved accuracy in estimates of capture probabilities provide more accurate abundance estimates that could impact management decisions, particularly with regard to bag limits, endangered species, and biological integrity assessments. First, we extended a popular model used in depletion studies to account for schooling behavior, a parameter not typically accounted for in ecological studies. We showed with simulated data that by accounting for schooling behavior in the beta-multinomial model, capture probabilities are more accurately estimated when compared to the multinomial model. Second, while our study organisms were stream fish, our beta-multinomial model is applicable for any species where aggregative behavior is a concern. For example, the removal protocol is often applied to salamanders (Jung et al. 2005) and insects (Russell et al. 2005), both of which exhibit a degree of aggregative behavior (Naumann 1975; Gautier et al. 2006). Finally, biological integrity metrics that are based on abundance measures can be misleading in light of overestimated abundance resulting in interpretation that a stream is healthier than estimated. Common methods of assessing biological integrity rely on sampling fish in wadeable streams (Simon and Dufour 1997) and many of the metrics used directly incorporate abundance and diversity, based on single pass electrofishing. Metrics that summarize the total catch per unit effort of individuals will inherently be biased if those individuals are composed of species with low capture probability (i.e., Percidae species) vs high capture probability (i.e., Catostomidae species). While the total observed number might be similar, the

actual abundance could be quite different depending on the capture probability of the individuals in the site and could result in the manager reaching a false conclusion about the true integrity rating.

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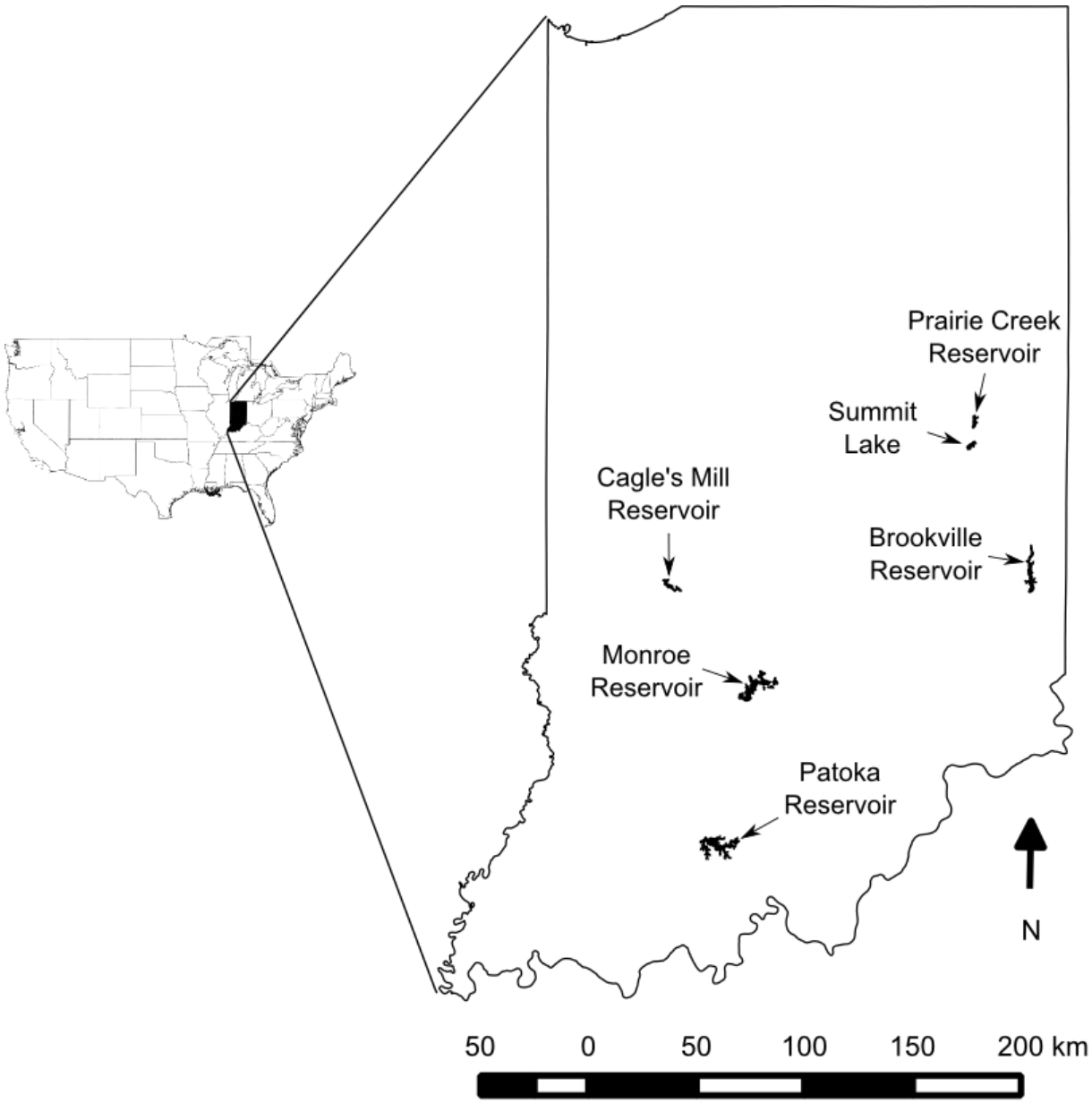

Figure 1. The location of Monroe Reservoir, Brookville Reservoir, Patoka Reservoir, Cagle's Mill Reservoir, Prairie Creek Reservoir, and Summit Lake.

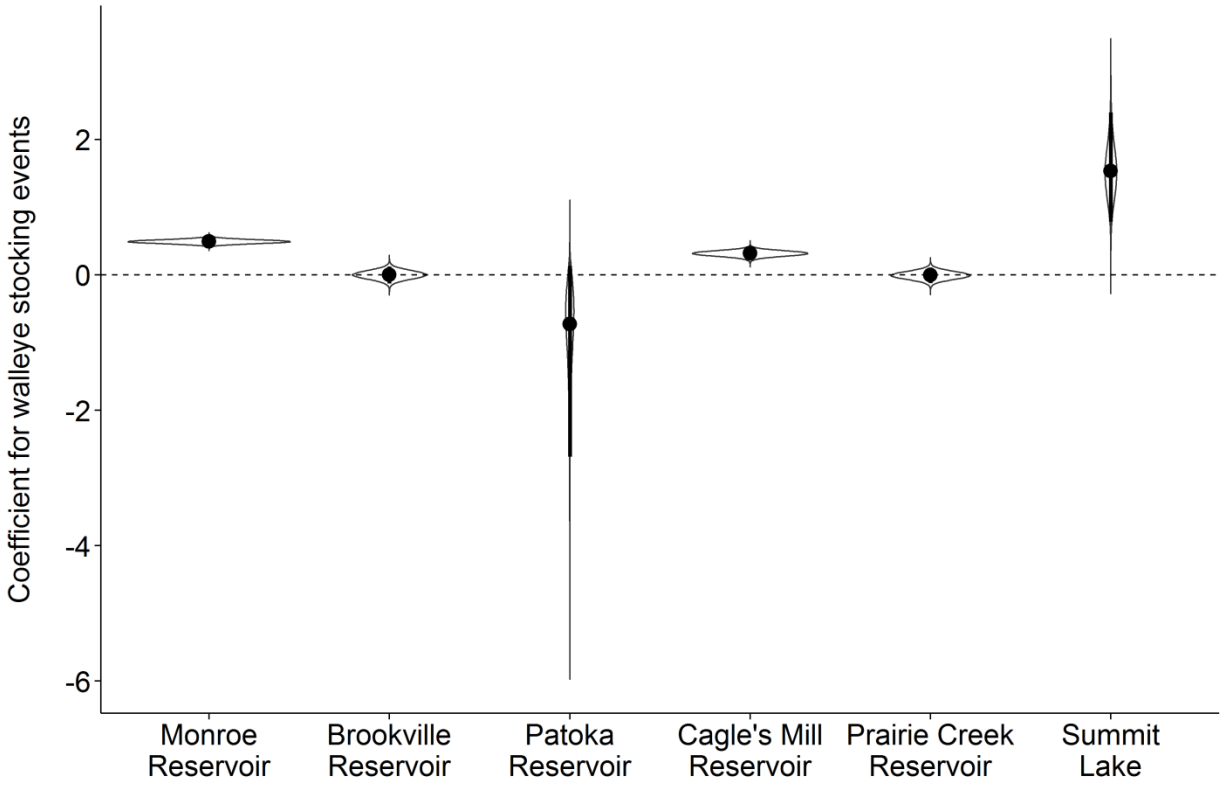

Figure 2. Violin plot of coefficient for Walleye stocking events for each reservoir. Black circles and vertical bars represent median and 95% credible interval of the posterior distribution. Width of violin area represent probability density of the parameter, wider areas suggest a higher probability for that coefficient value.

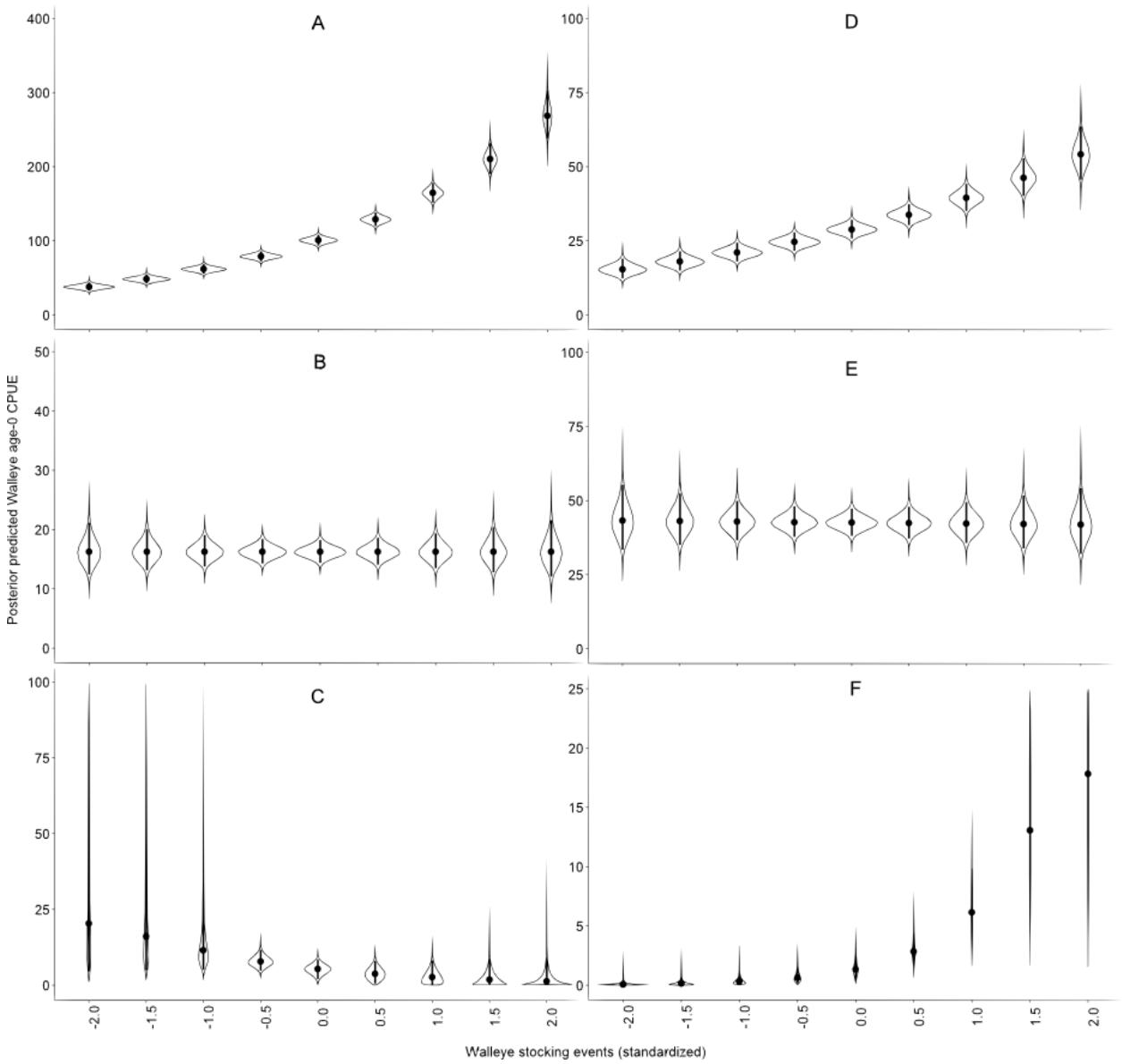

Figure 3. Posterior predicted Walleye catch-per-unit-effort (CPUE) at age-0 in the fall based on average moronid stocking abundance, average maximum spring/summer discharge/rain, and variable Walleye stocking events at each reservoir. Stocking events are standardized to a mean 0 and unit standard deviation. Thus, 0 indicates average stocking events for the specific reservoir. A = Monroe Reservoir, B = Brookville Reservoir, C = Patoka Reservoir, E = Cagle's Mill Reservoir, E = Prairie Creek Reservoir, and F = Summit Lake.

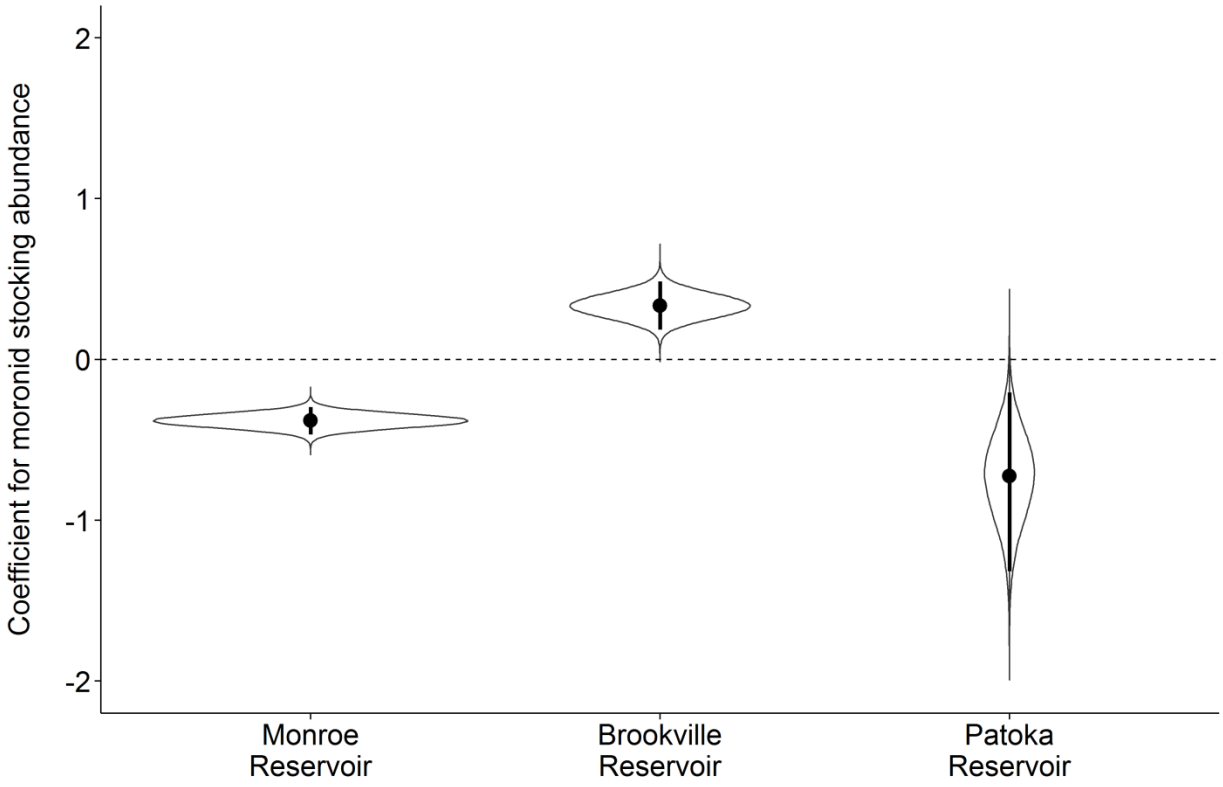

Figure 4. Violin plot of coefficient for moronid stocking abundance for each reservoir. Black circles and vertical bars represent median and 95% credible interval of the posterior distribution. Width of violin area represent probability density of the parameter, wider areas suggest a higher probability for that coefficient value.

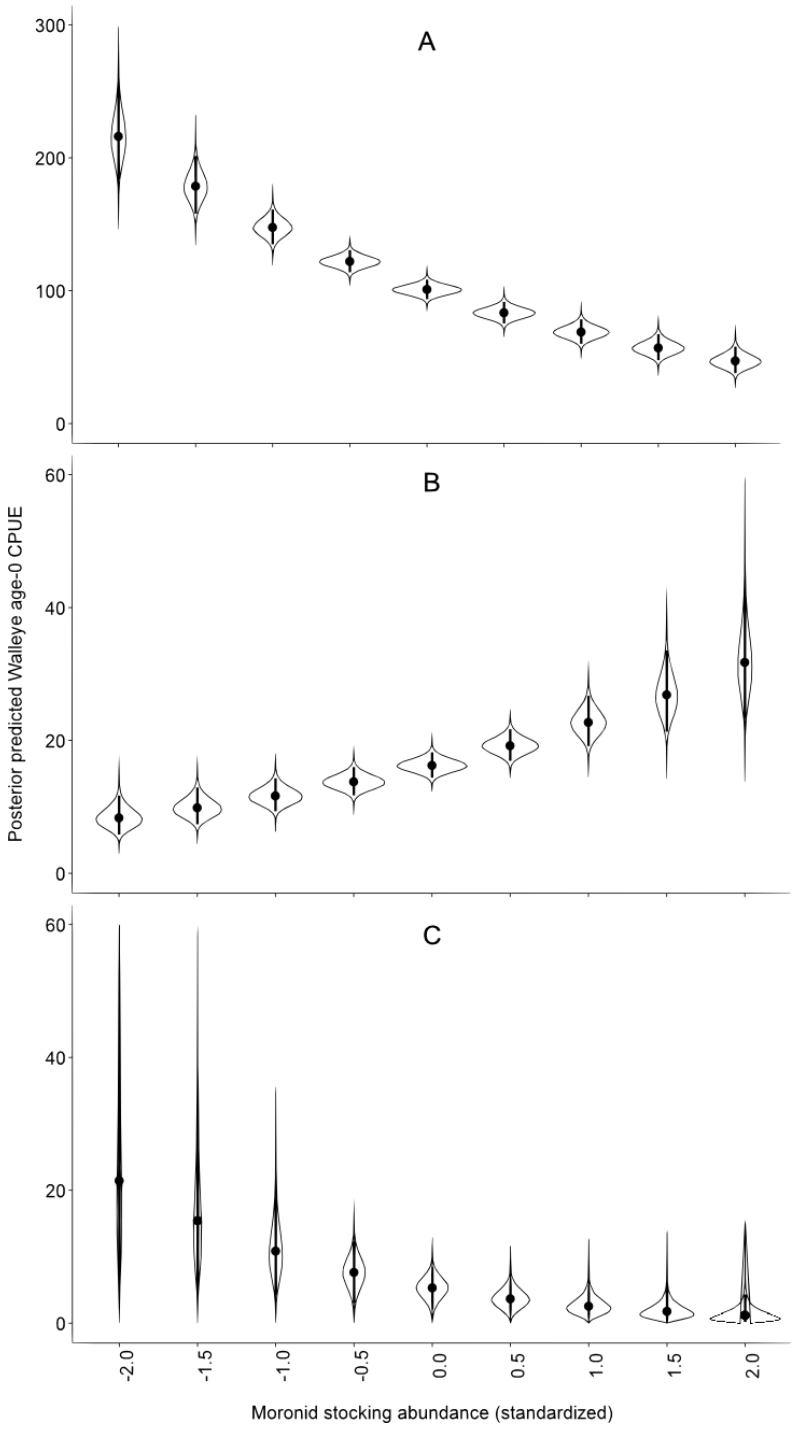

Figure 5. Posterior predicted Walleye catch-per-unit-effort (CPUE) at age-0 in the fall based on average Walleye stocking events, average maximum spring/summer discharge/rain, and variable moronid stocking abundance at each reservoir. Moronid stocking abundance is standardized to a mean 0 and unit standard deviation. Thus, 0 indicates average moronid stocking abundance for the specific reservoir. A = Monroe Reservoir, B = Brookville Reservoir, C = Patoka Reservoir.

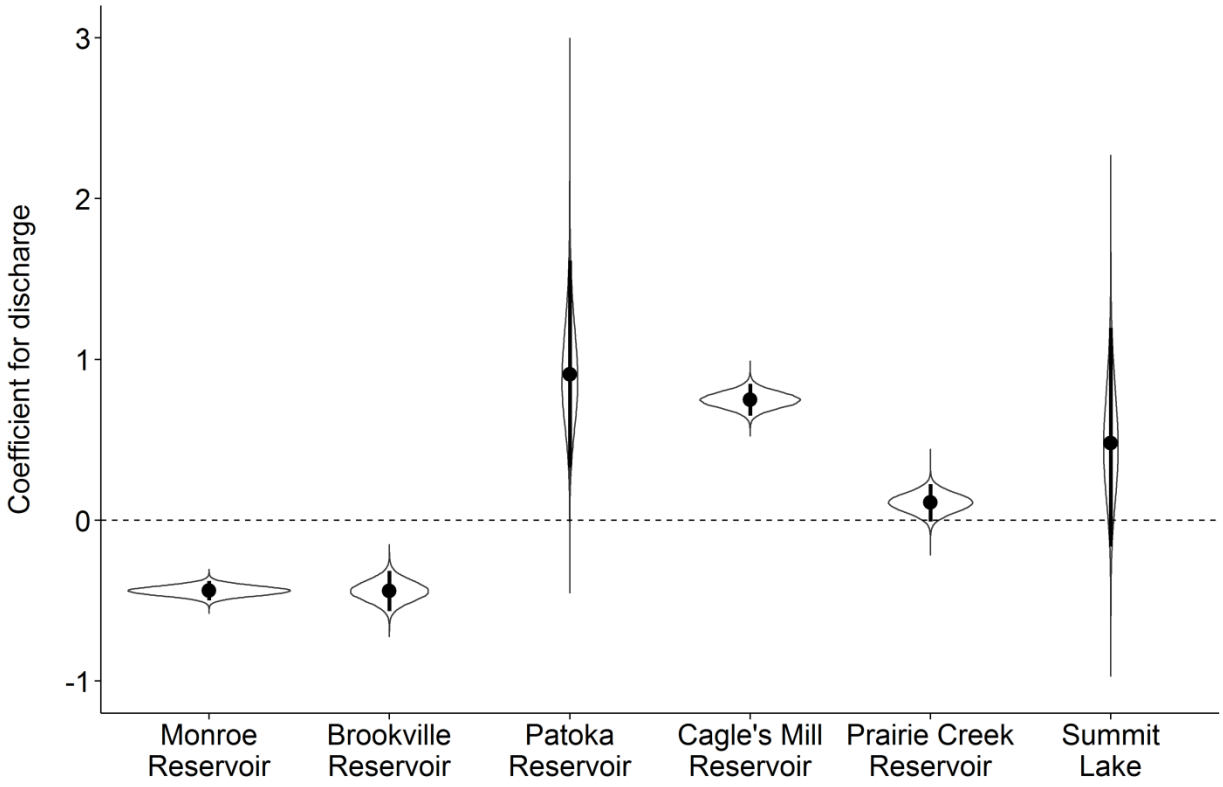

Figure 6. Violin plot of coefficient for maximum spring/summer discharge/rain total for each reservoir. Black circles and vertical bars represent median and 95% credible interval of the posterior distribution. Width of violin area represent probability density of the parameter, wider areas suggest a higher probability for that coefficient value.

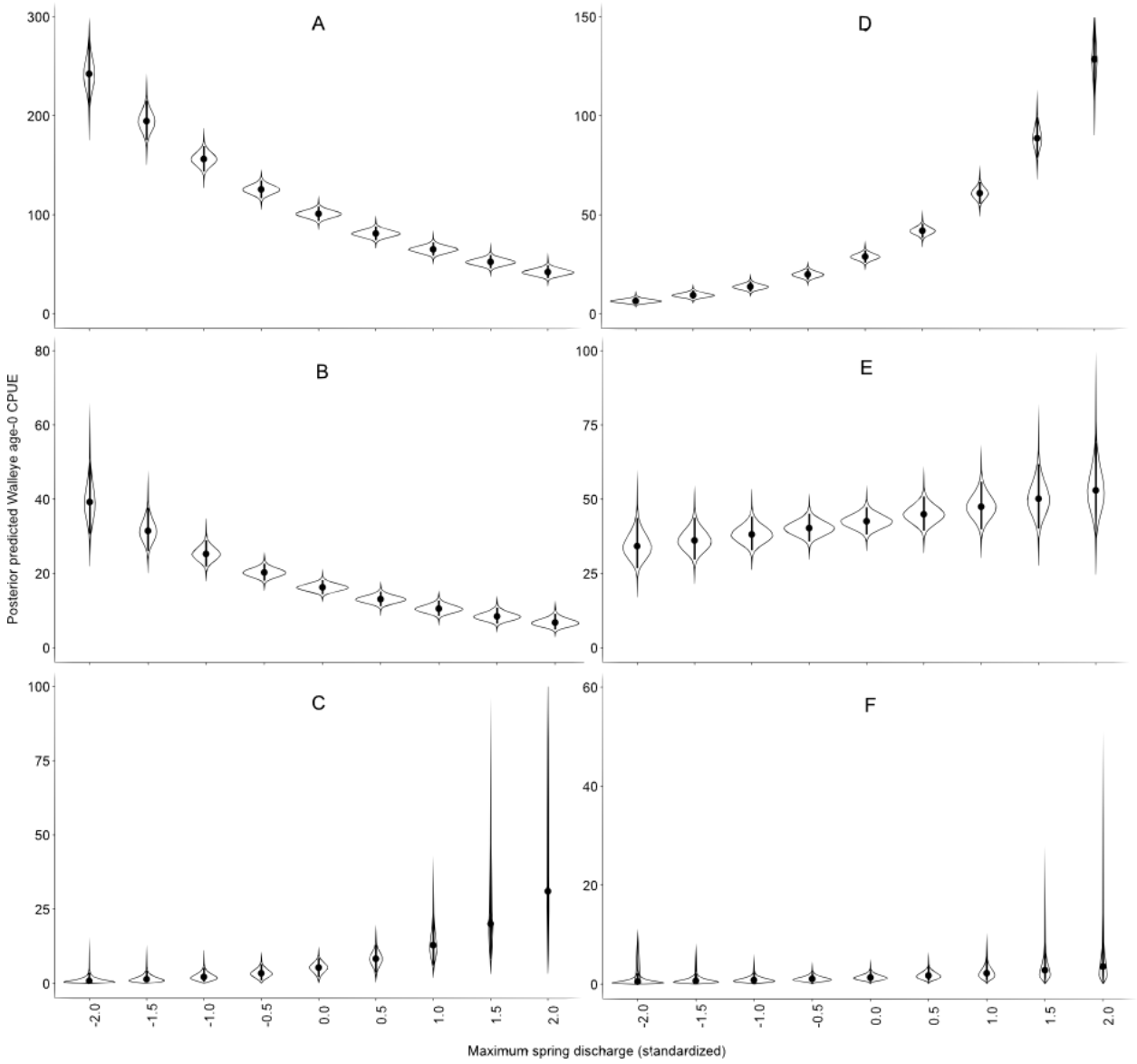

Figure 7. Posterior predicted Walleye catch-per-unit-effort (CPUE) at age-0 in the fall based on average Walleye stocking events, average moronid stocking abundance, and variable maximum spring/summer discharge/rain at each reservoir. Maximum spring/summer discharge/rain is standardized to a mean 0 and unit standard deviation. Thus, 0 indicates average maximum spring/summer discharge/rain for the specific reservoir. A = Monroe Reservoir, B = Brookville Reservoir, C = Patoka Reservoir, E = Cagle's Mill Reservoir, E = Prairie Creek Reservoir, and F = Summit Lake.

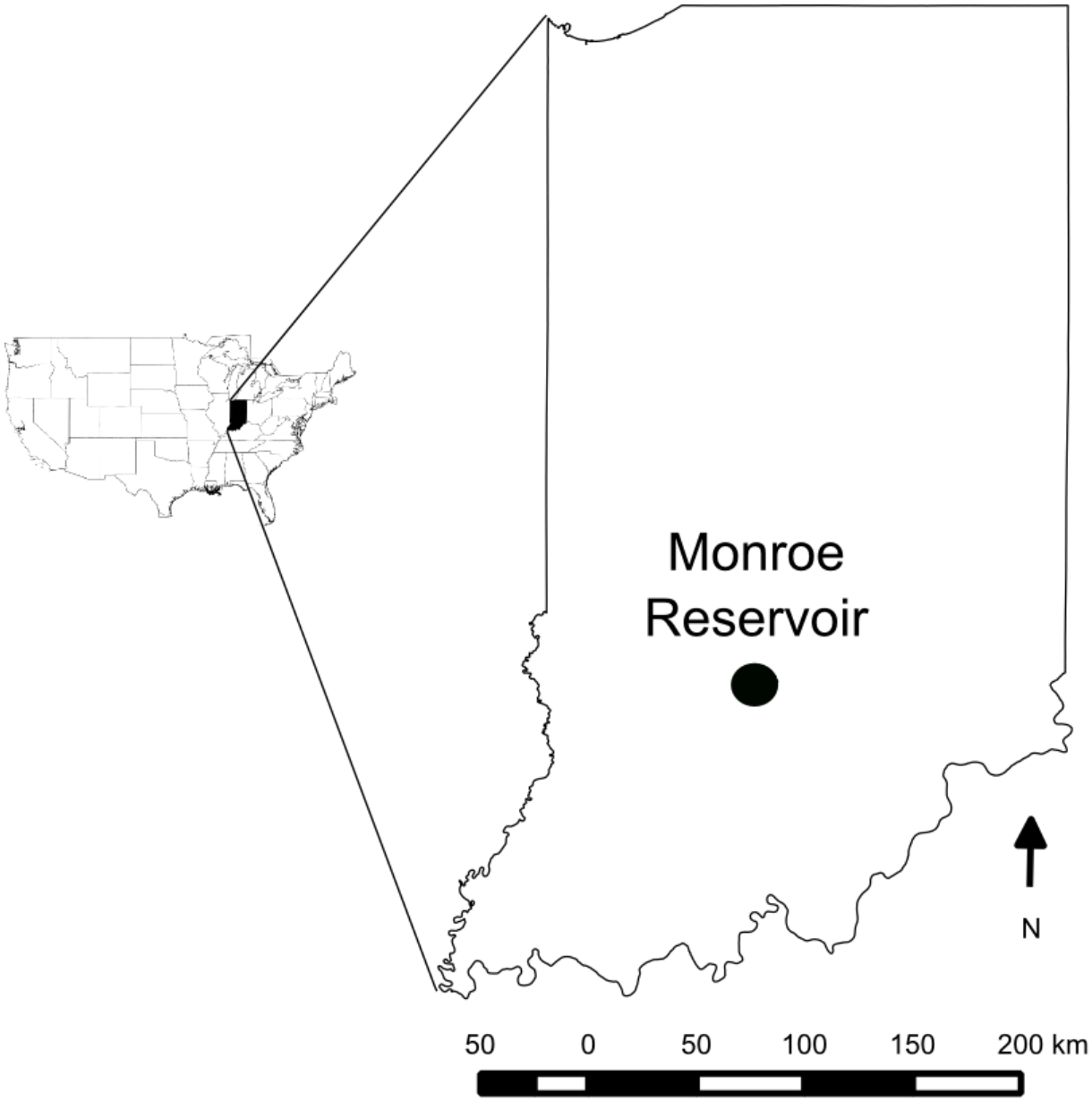

Figure 8. The location of Monroe Reservoir.

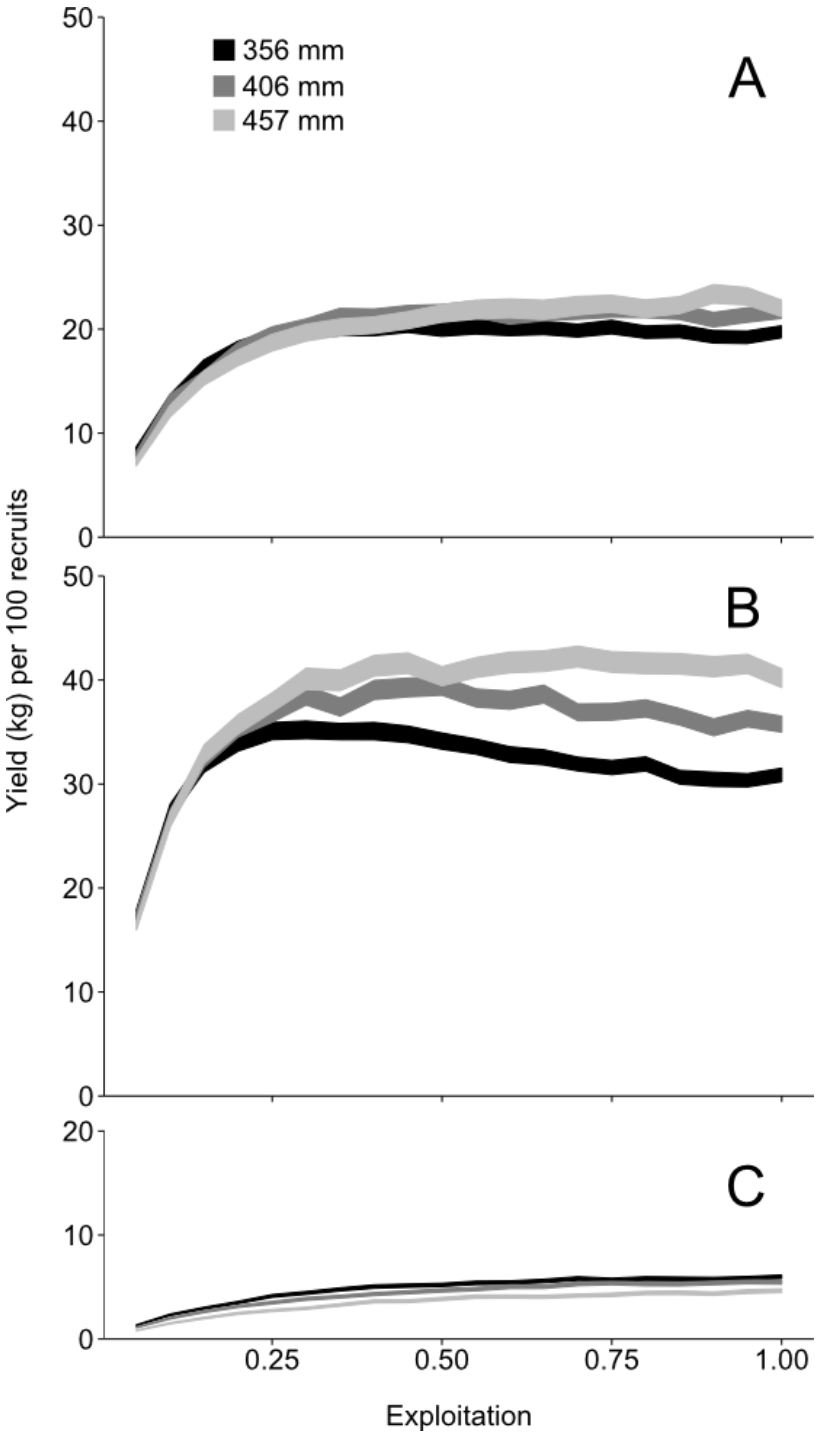

Figure 9. Yield (kg) per 100 recruits of Walleye as a function of exploitation ranging from 0.05 to 1.00 with three minimum length limits (356, 406, and 457 mm) and conditional natural mortality estimated from the data (A), set equal to 0.20 (B), and set equal to 0.50 (C). Width of bars represents ± 2 * standard error.

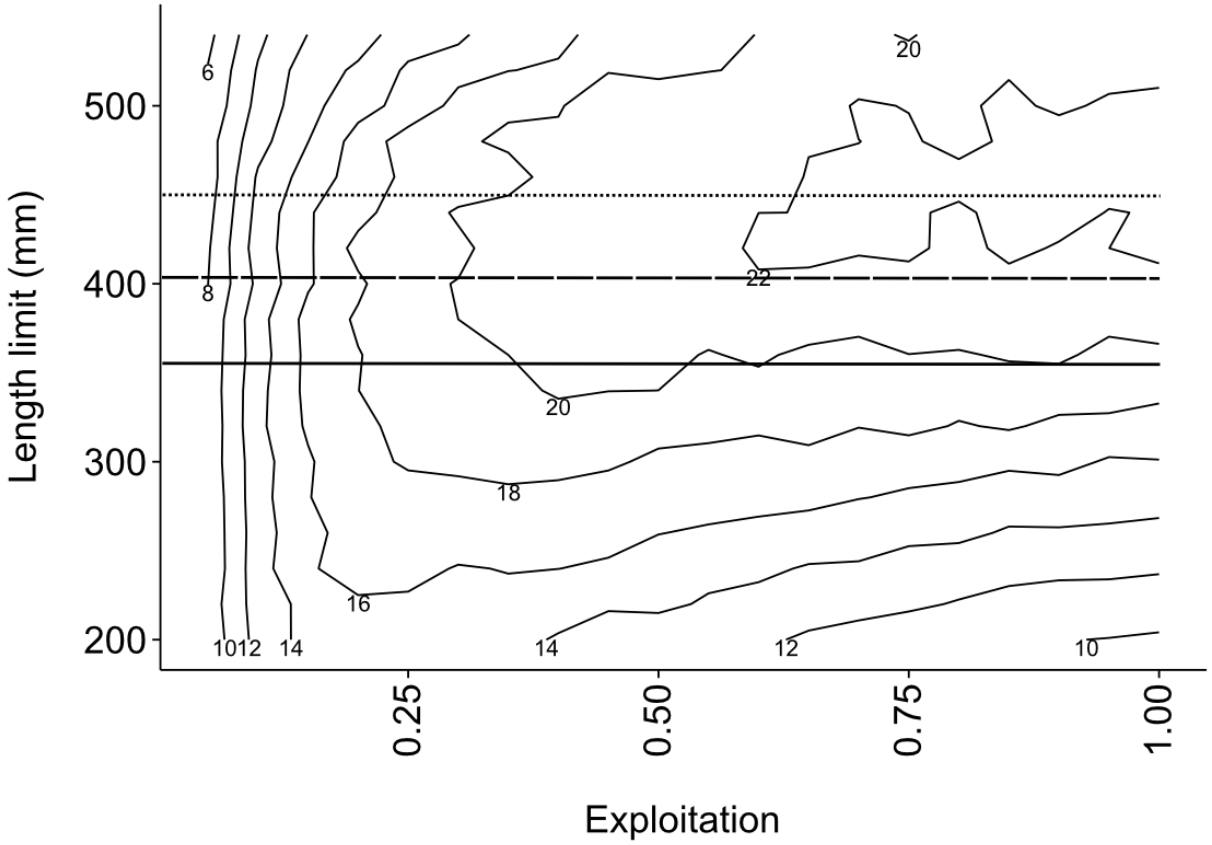

Figure 10. Yield (kg) isopleth of Walleye constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 550 mm and based on conditional natural mortality estimated from the data (Table 6). Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

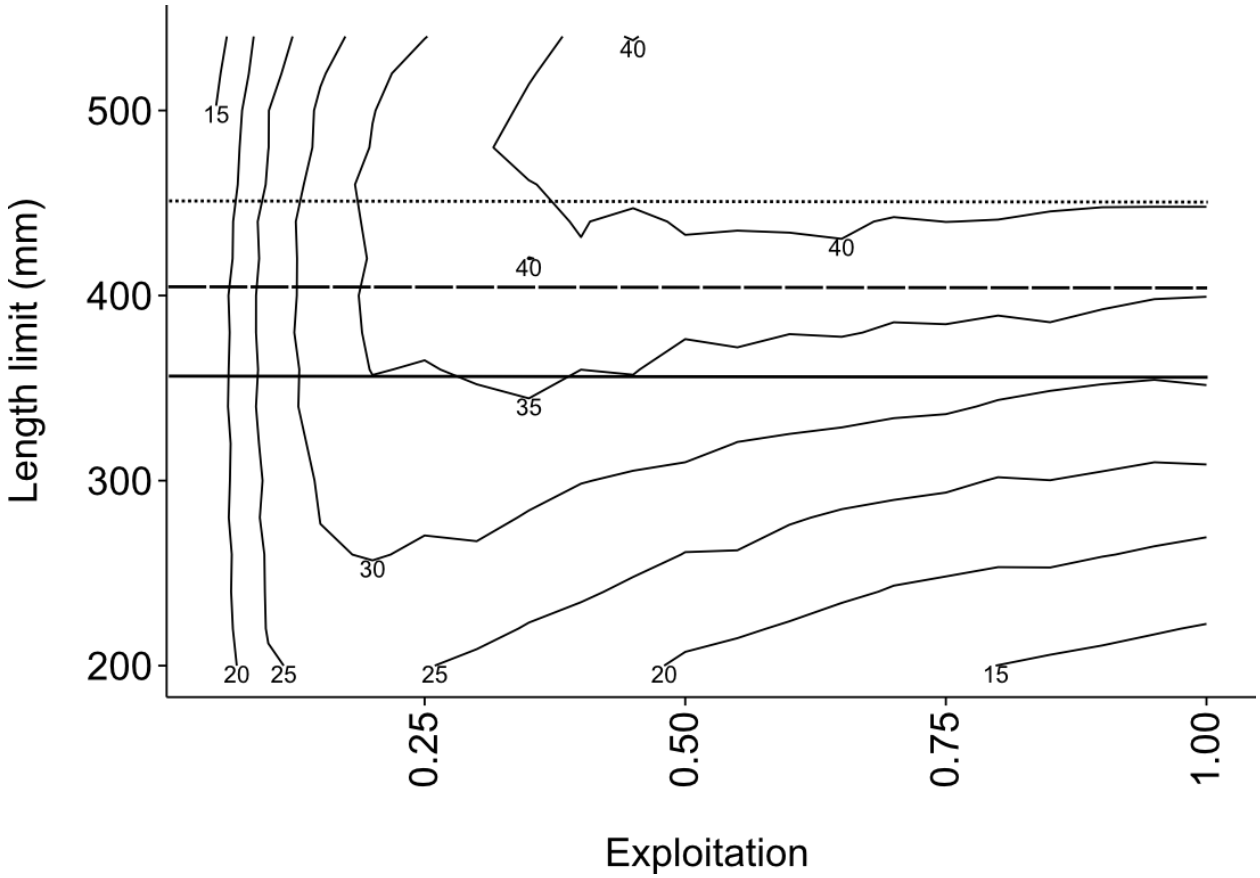

Figure 11. Yield (kg) isopleth of Walleye constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 550 mm and based on conditional natural mortality set equal to 0.20. Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

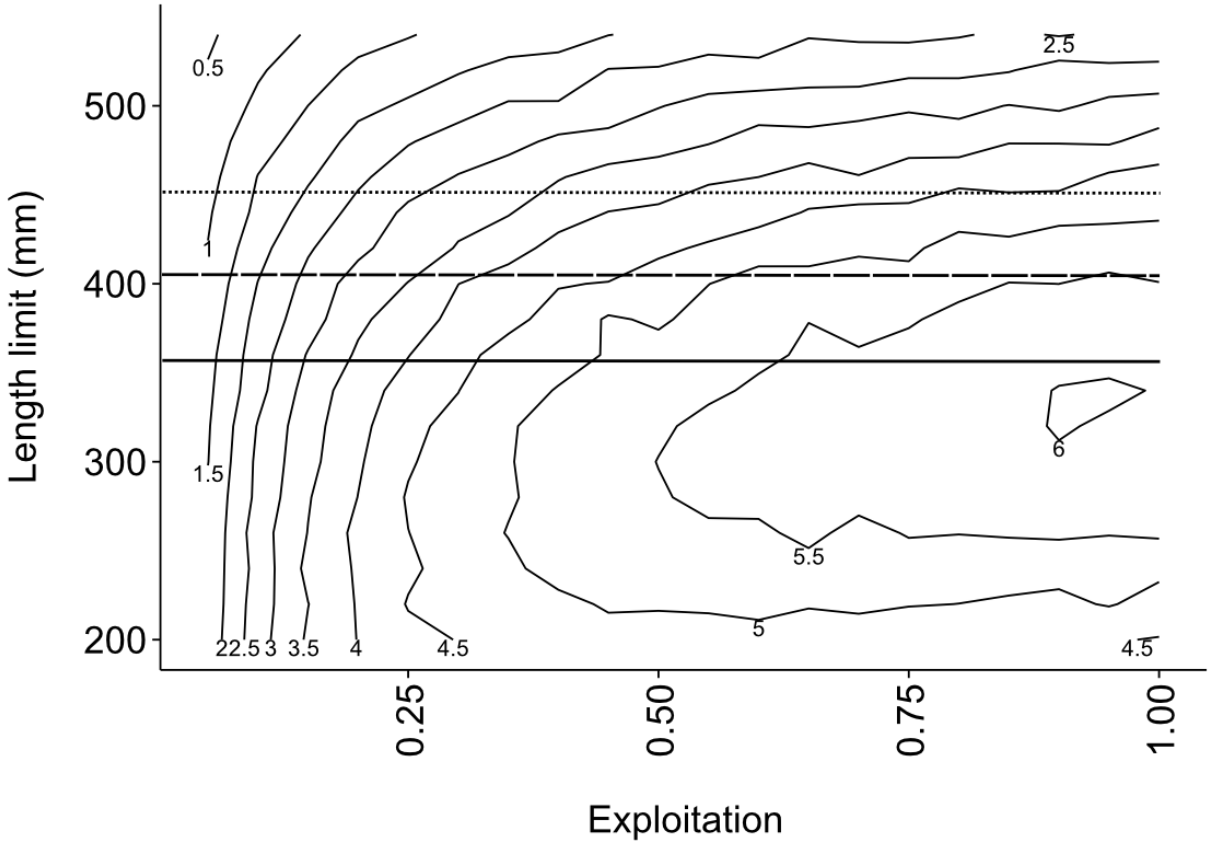

Figure 12. Yield (kg) isopleth of Walleye constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 550 mm and based on conditional natural mortality set equal to 0.50. Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

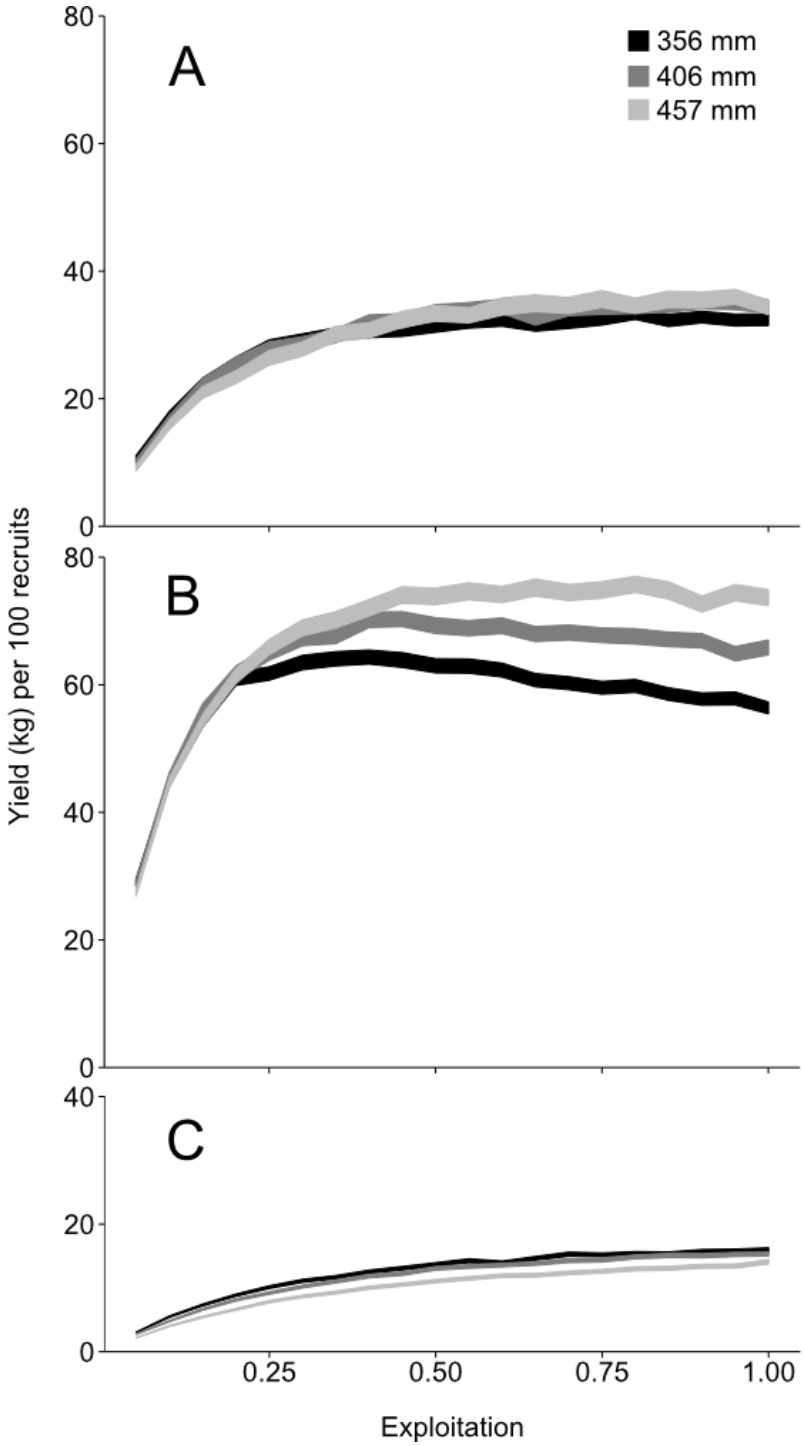

Figure 13. Yield (kg) per 100 recruits of hybrid striped bass as a function of exploitation ranging from 0.05 to 1.00 and based on three minimum length limits (356, 406, and 457 mm) and conditional natural mortality estimated from the data (A), set equal to 0.20 (B), and set equal to 0.50 (C). Width of bars represents ± 2 * standard error.

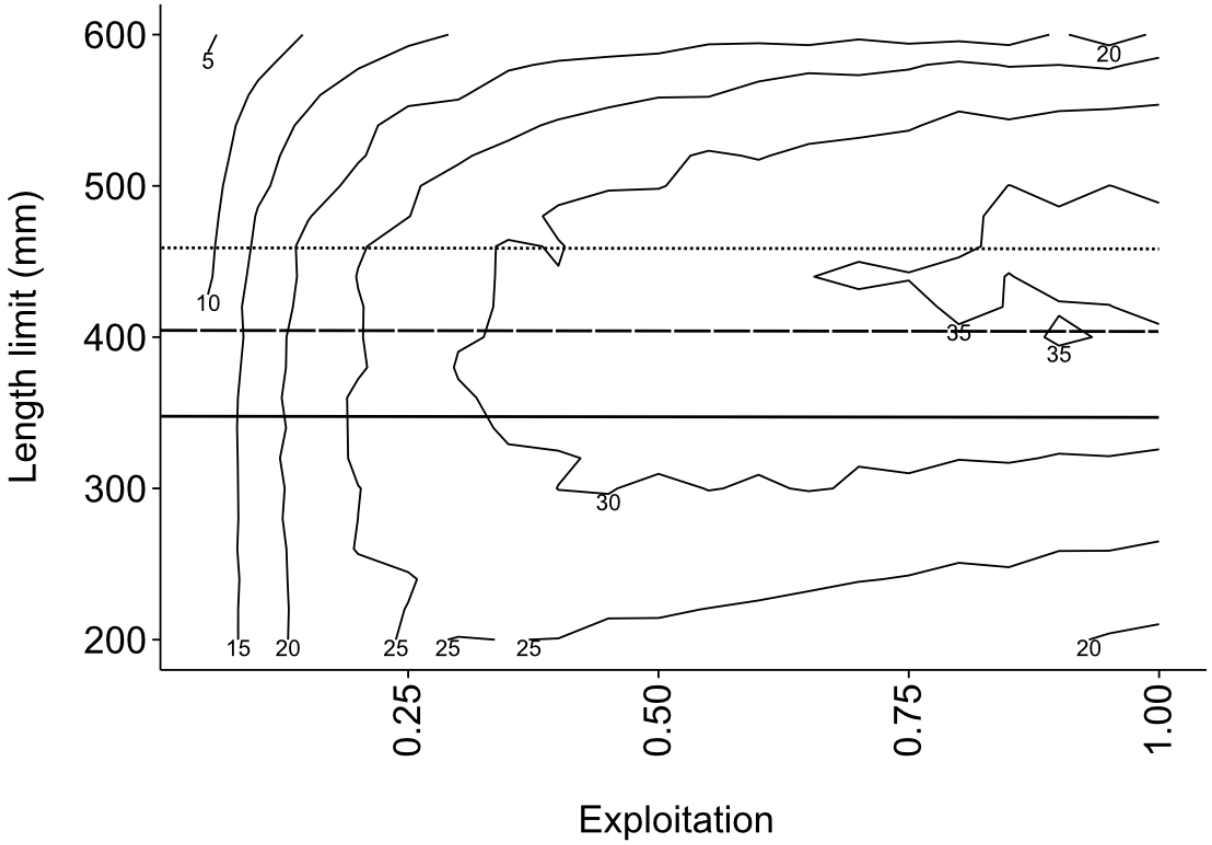

Figure 14. Yield (kg) isopleth of hybrid striped bass constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 600 mm and based on conditional natural mortality estimated from the data (Table 6). Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

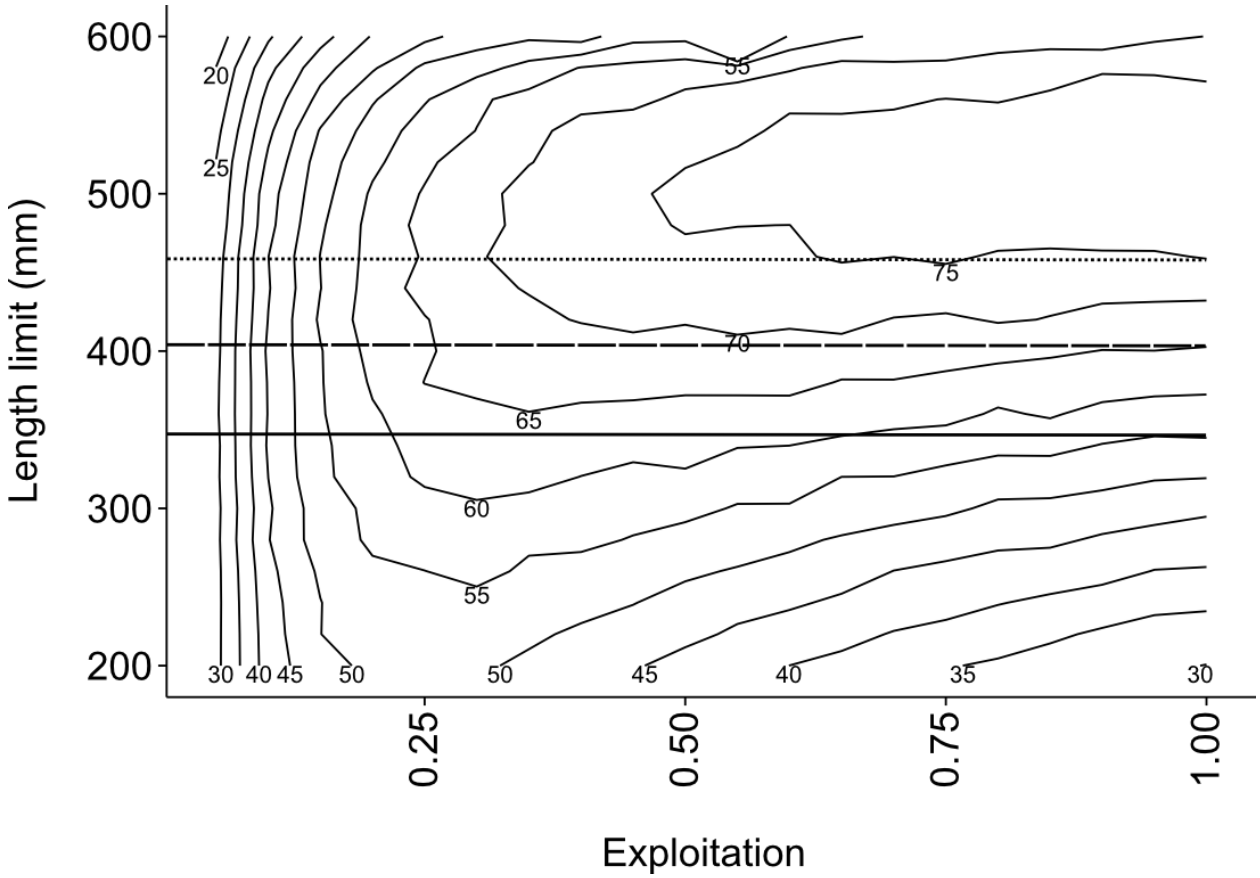

Figure 15. Yield (kg) isopleth of hybrid striped bass constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 600 mm and based on conditional natural mortality set equal to 0.20. Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

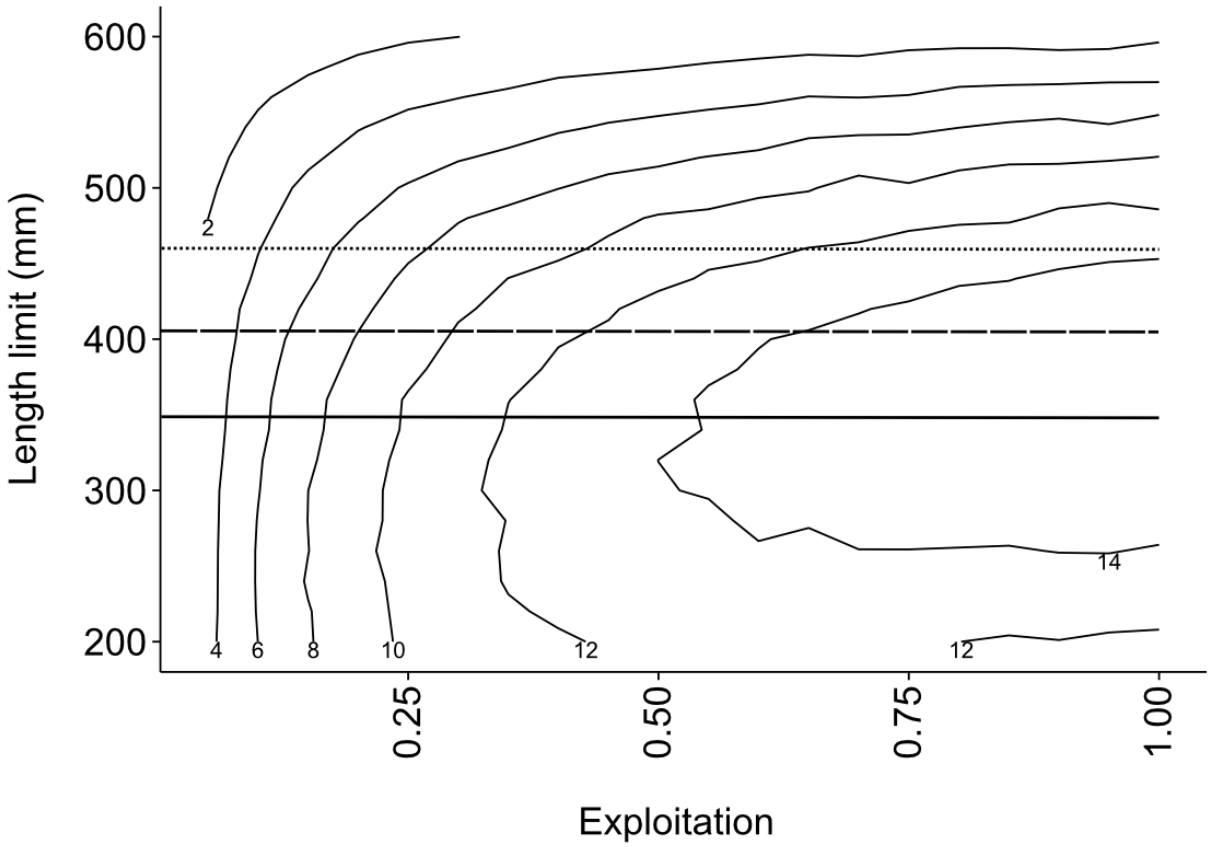

Figure 16. Yield (kg) isopleth of hybrid striped bass constructed from the yield-per-recruit model under exploitation rates ranging from 0.05 to 1.00 and minimum harvest length limits ranging from 200 to 600 mm and based on conditional natural mortality set equal to 0.50. Horizontal solid, dashed, and dotted lines represent a 356, 406, and 457 mm minimum size limit.

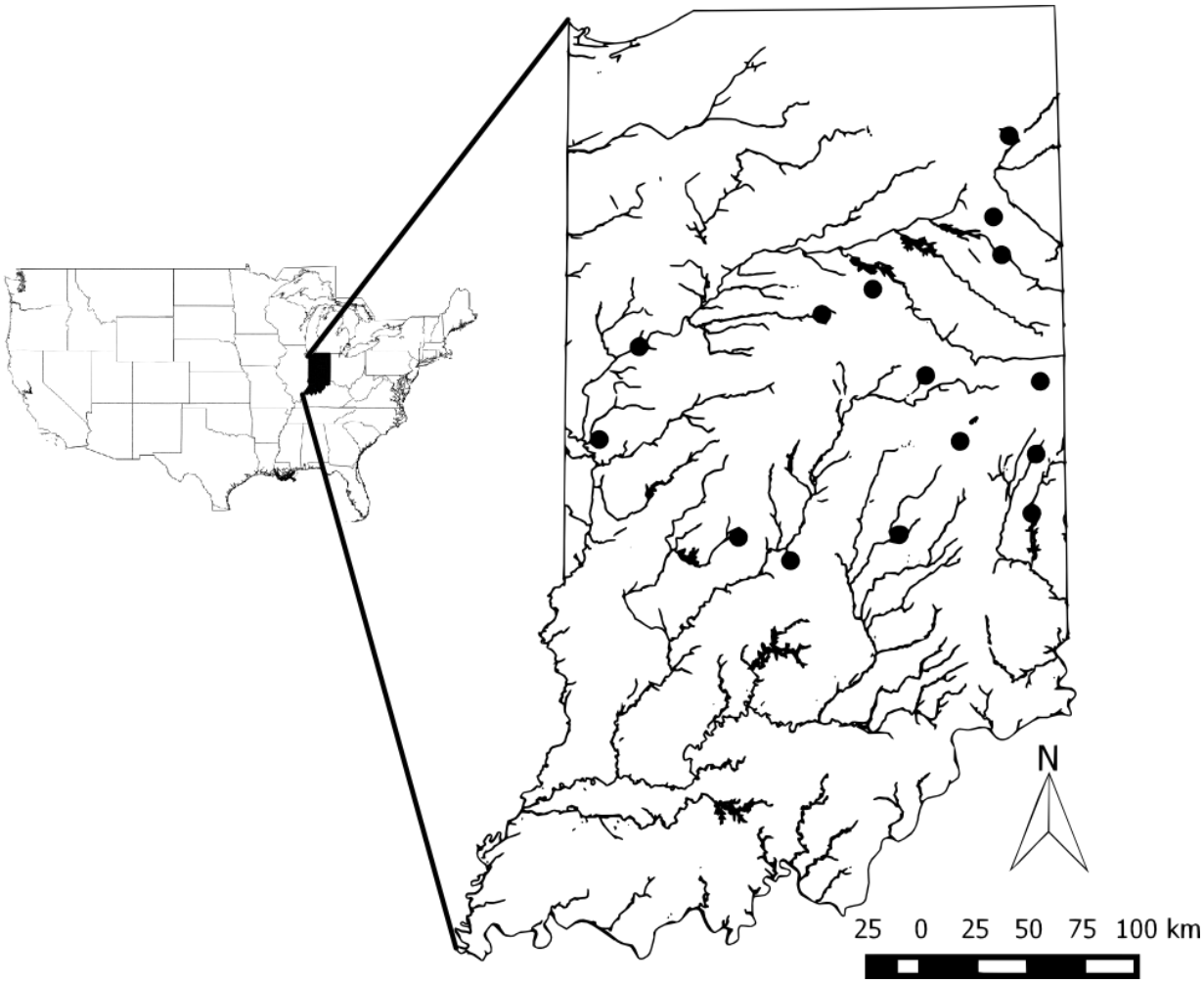

Figure 17. Sampling sites for multi-pass depletion estimates of stream fish assemblage.

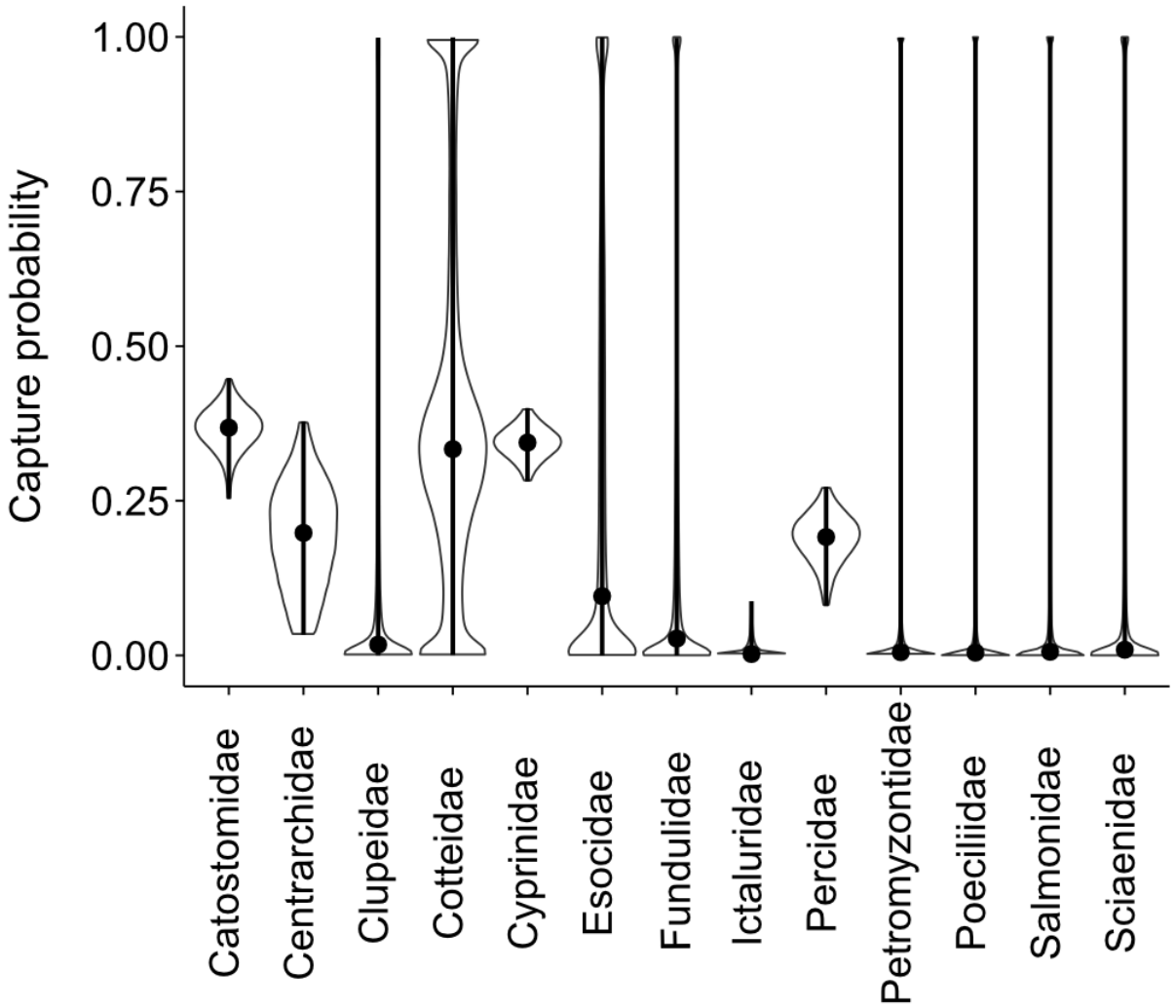

Figure 18. Family level capture probabilities estimated from the multinomial model. Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

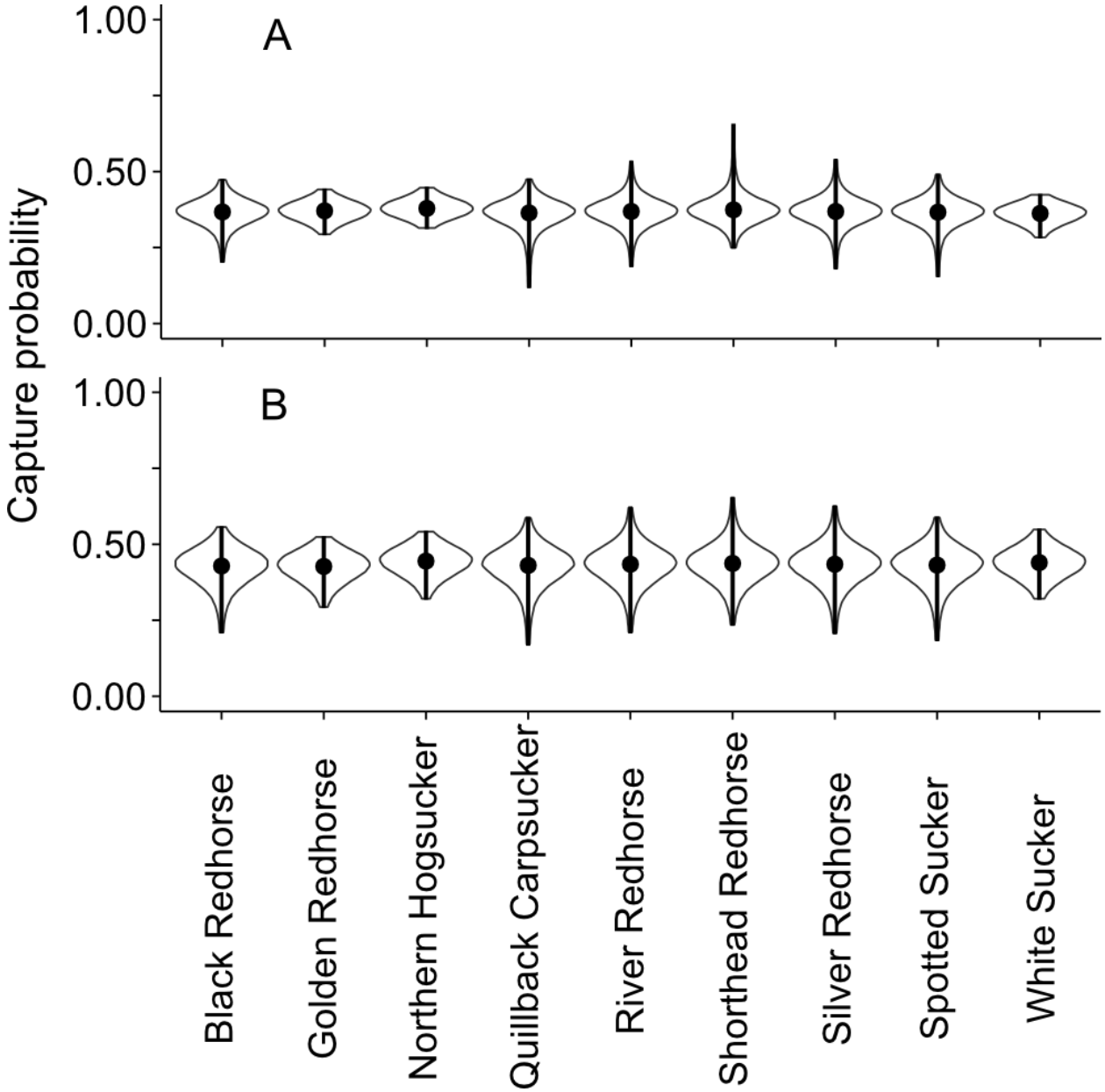

Figure 19. Catostomidae species capture probabilities estimated from the multinomial model (A) and beta-multinomial model (B). So Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

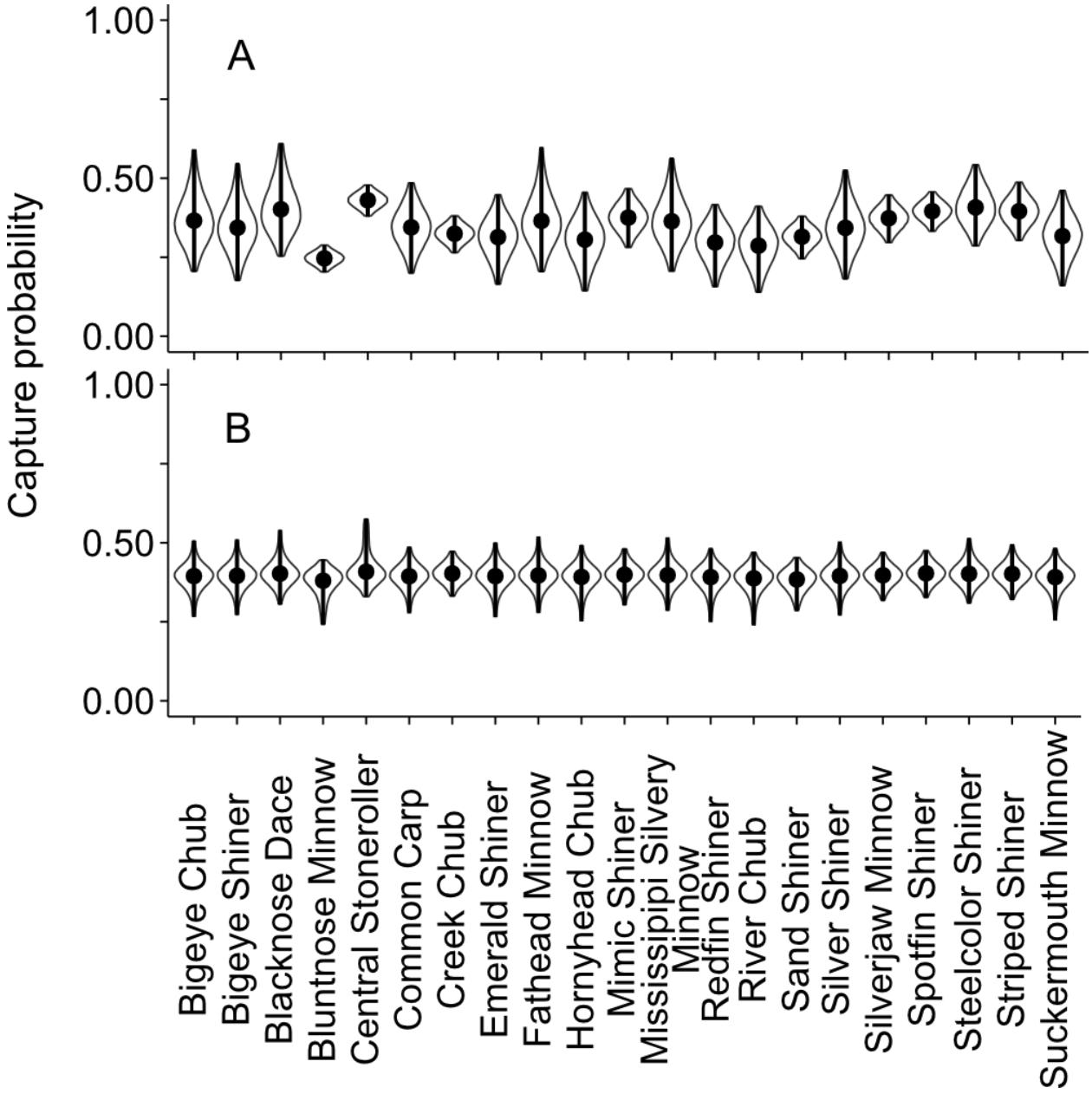

Figure 20. Cyprinidae species capture probabilities estimated from the multinomial model (A) and beta-multinomial model (B). So Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

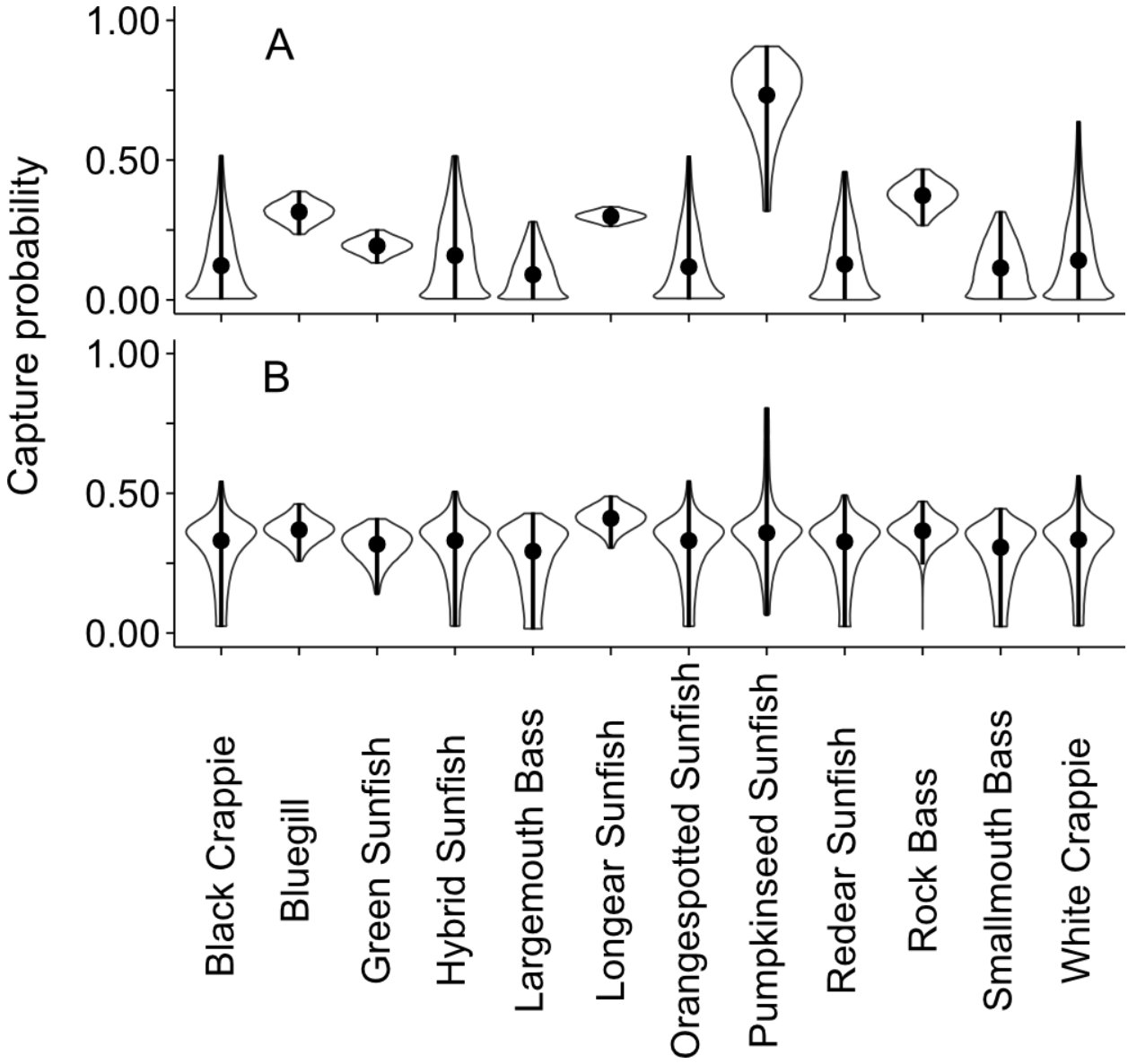

Figure 21. Centrarchidae species capture probabilities estimated from the multinomial model (A) and beta-multinomial model (B). So Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

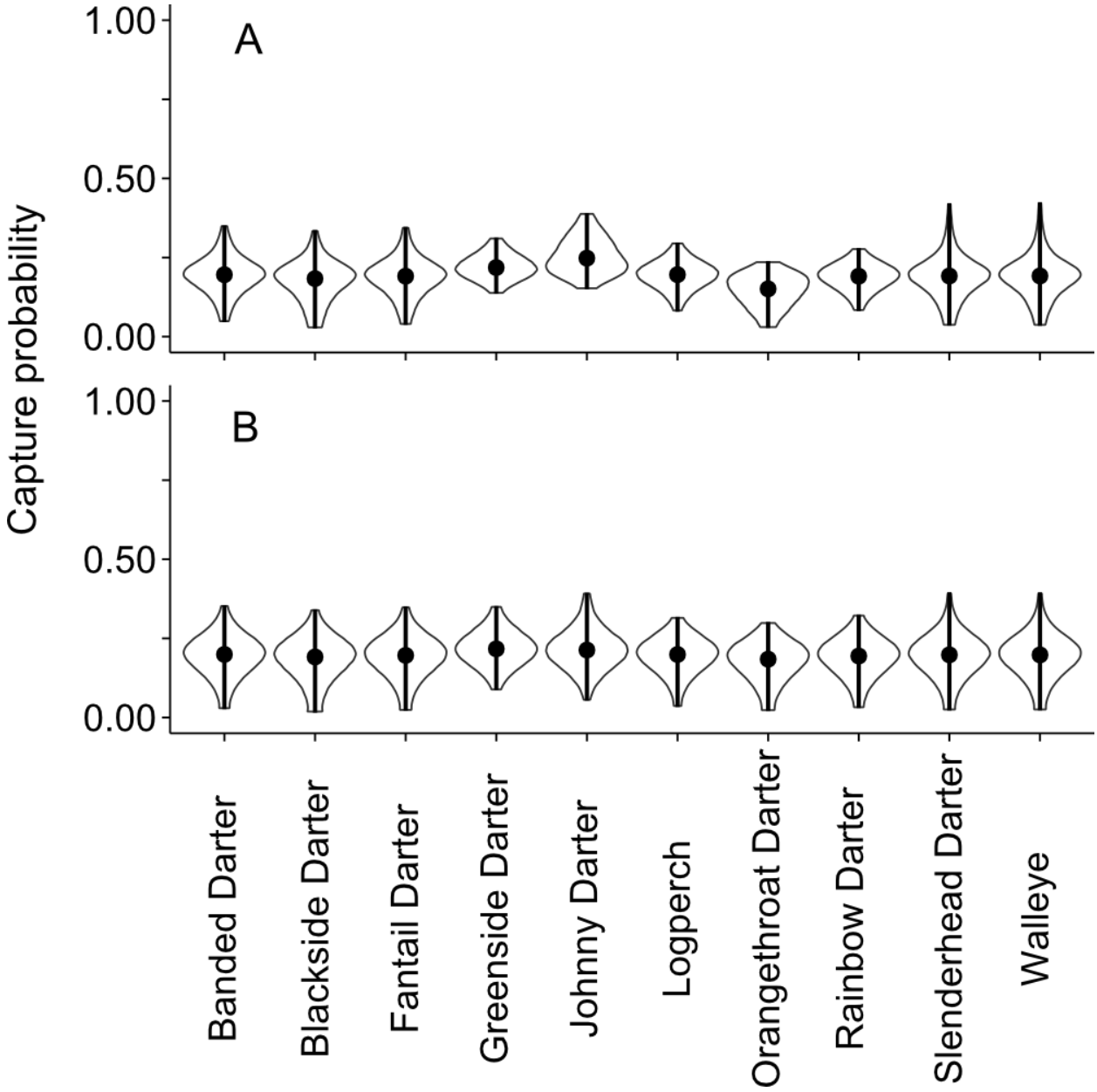

Figure 22. Percidae species capture probabilities estimated from the multinomial model (A) and beta-multinomial model (B). So Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

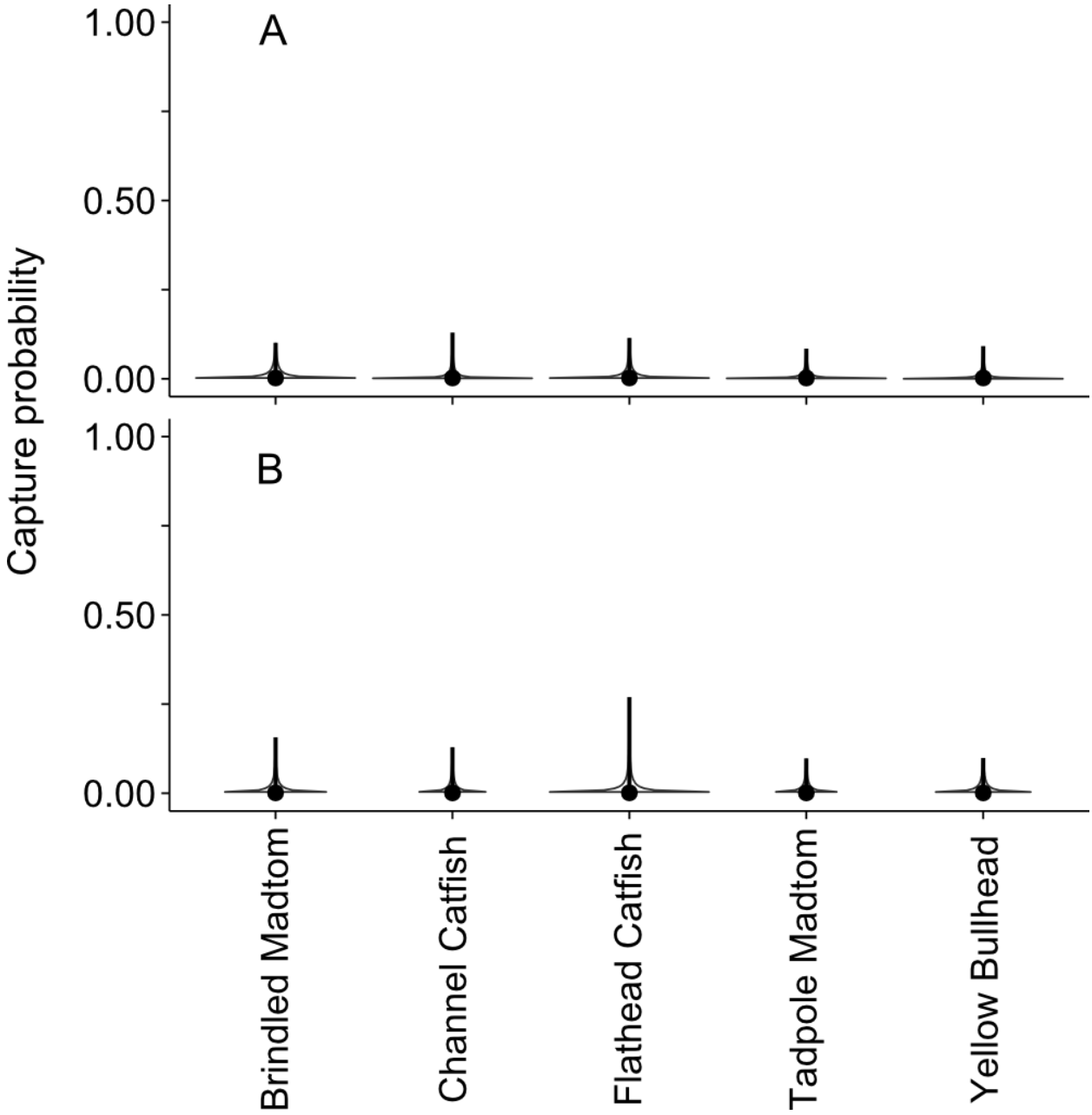

Figure 23. Ictaluridae species capture probabilities estimated from the multinomial model (A) and beta-multinomial model (B). So Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. Violin plots represent the probability mass associated with the capture probability. The widest cross-sectional width of the violin plots represents the capture probability with the highest likelihood. The violin plots have been trimmed at the ends of the 95% credible intervals.

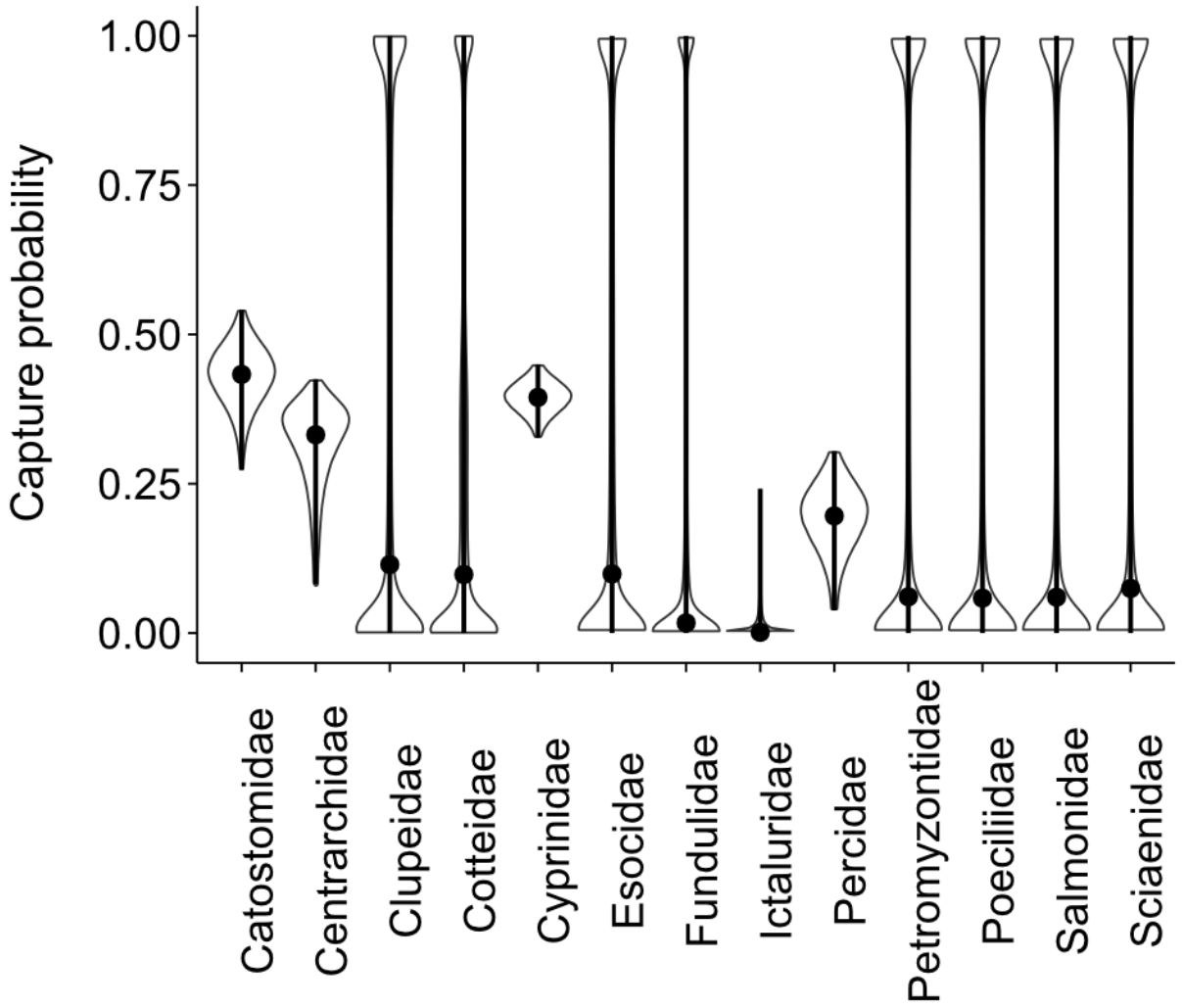

Figure 24. Family level capture probabilities estimated from the beta-multinomial model. Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. The violin plots have been trimmed at the ends of the 95% credible intervals.

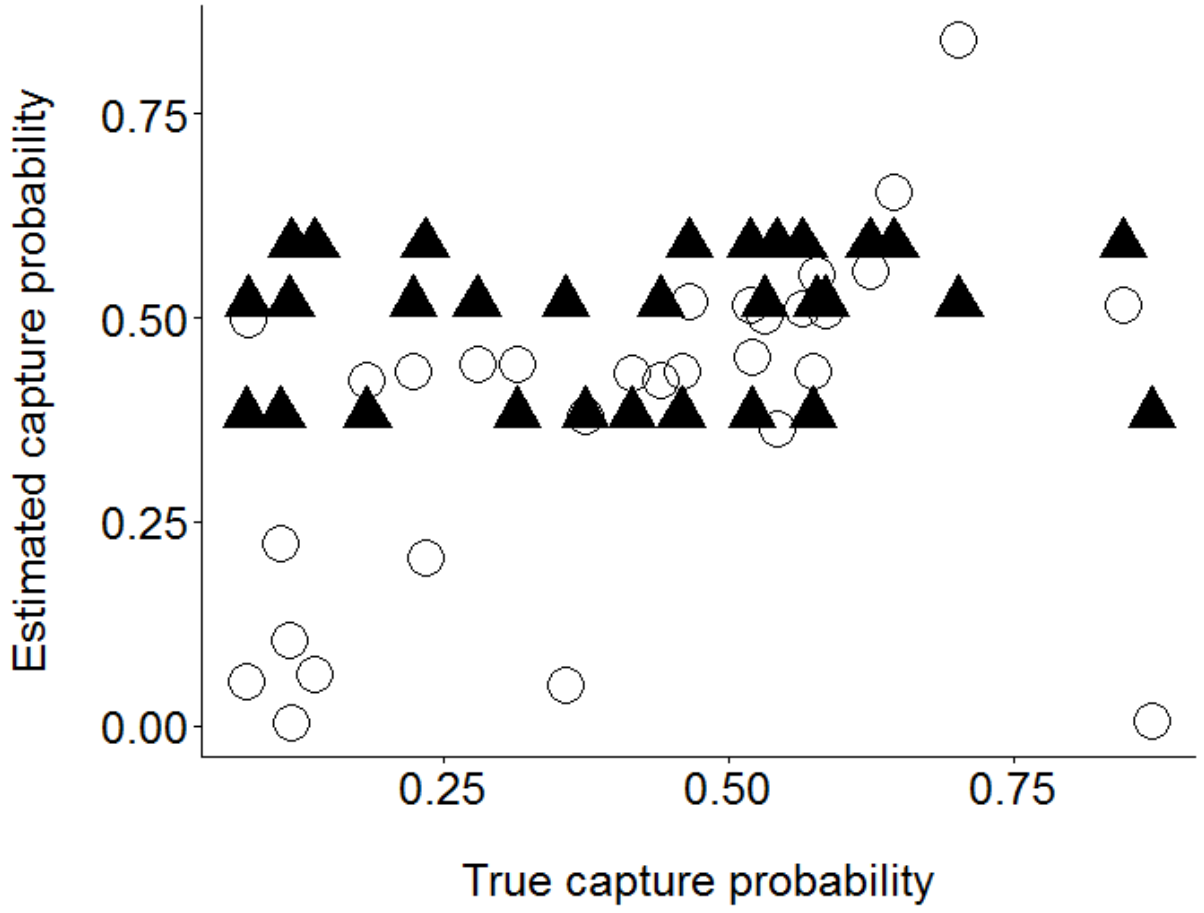

Figure 25. Median values from the posterior distribution of estimated capture probabilities vs the true capture probability value from simulated data. Solid triangles represent estimates from the multinomial model and open circles represent estimates from the beta-multinomial model.

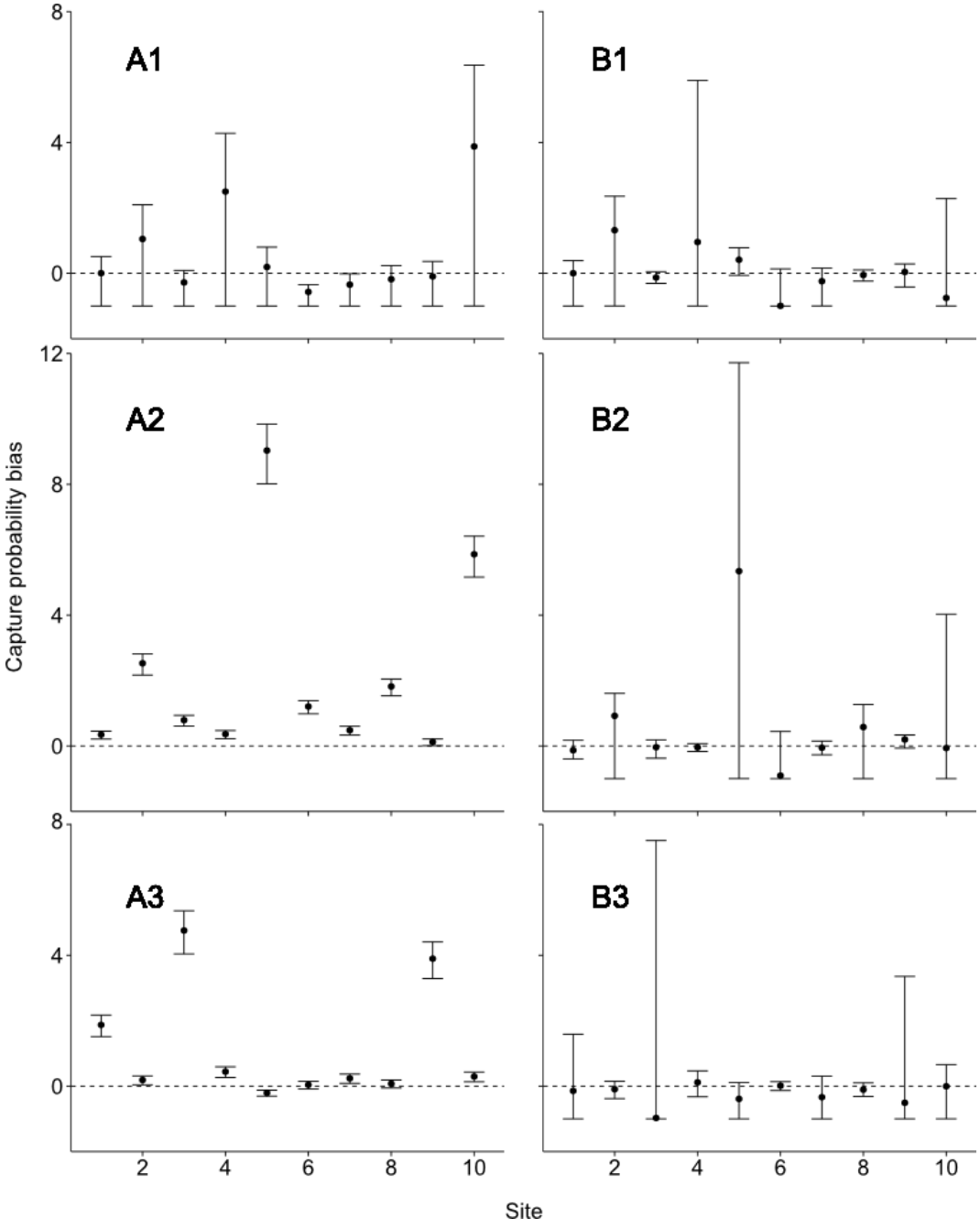

Figure 26. Relative bias of capture probability for three species and ten sites. Solid points are the medians of the posterior distribution and error bars represent the bounds of the 95% credible intervals. A1, A2, and A3 are relative bias estimates for three species at ten sites using the multinomial model and B1, B2, and B3 are relative bias estimates for three species at ten sites using the beta-multinomial model. The horizontal dashed lines indicate the points where bias in the estimates are 0. If credible intervals overlap this line, it is concluded that there is no credible difference between the distribution of estimates and the true value. The violin plots have been trimmed at the ends of the 95% credible intervals.

Table 1. Description of study area. SDF = shoreline development factor calculated as the ratio of the actual perimeter of the reservoir to the expected perimeter of a perfect circle with the same area.

Reservoir	Latitude/Longitude	Hectares	SDF	Mean depth (m)	Maximum depth (m)	Volume (m^3)	Sample years (N)
Monroe Reservoir	39.0082/-86.5116	4,350	6.9	7.6	16.5	$3.29 * 10^8$	1994-2001 (9)
Brookville Reservoir	39.4394/-85.0000	2,129	5.2	9.1	35.4	$1.91 * 10^8$	1981-2007 (20)
Patoka Reservoir	38.4343/-86.7075	3,561	10.7	6.4	15.8	$2.22 * 10^8$	2008-2012 (5)
Cagle's Mill Reservoir	39.4864/-86.9173	567	5.4	5.8	17.0	$3.47 * 10^7$	1990-2008 (14)
Prairie Creek Reservoir	40.1471/-85.2913	507	2.6	5.5	9.8	$2.69 * 10^7$	2001-2009 (8)
Summit Lake	40.0236/-85.3257	338	4.5	6.7	14.3	$2.45 * 10^7$	2000-2007 (7)

Table 2. Watershed land use (percentage of total area) surrounding study reservoirs. Land use data from the Indiana GAP analysis project.

Reservoir	HUC unit	Barren land	Cultivated crops	Deciduous forest	Developed	Emergent herbaceous wetlands	Evergreen forest	Grasslands/ herbaceous	Mixed forest	Open water	Pasture / hay	Shrub/ scrub	Woody wetlands
Monroe Reservoir	11	0.5%	1.0%	72.4%	1.6%	< 0.1%	1.3%	1.6%	0.1%	17.4%	3.9%	0.3%	< 0.1%
Brookville Reservoir	11	< 0.1%	48.7%	24.6%	13.2%	0.2%	0.3%	0.8%	< 0.1%	3.0%	9.1%	< 0.1%	< 0.1%
Patoka Reservoir	11	0.3%	3.8%	65.2%	3.9%	< 0.1%	1.6%	4.5%	0.1%	8.1%	12.0%	0.6%	< 0.1%
Cagle's Mill Reservoir	11	0.02%	61.3%	22.8%	5.4%	< 0.1%	0.2%	1.3%	< 0.1%	1.1%	7.8%	< 0.1%	< 0.1%
Prairie Creek Reservoir	12	< 0.1%	63.5%	9.4%	5.9%	< 0.1%	< 0.1%	2.1%	< 0.1%	12.1%	6.7%	0.2%	< 0.1%
Summit Lake	12	< 0.1%	48.6%	9.9%	5.8%	0.7%	< 0.1%	2.5%	< 0.1%	13.2%	19.3%	0.1%	< 0.1%

Table 3. Data summary statistics, mean and standard error. Walleye stocking at Monroe Reservoir, Prairie Creek Reservoir, and Summit Lake are number of fingerlings hectare^{-1}; Walleye stocking at Brookville Reservoir, Patoka Reservoir, and Cagle's Mill Reservoir are number of fry hectare^{-1}; moronid stocking at Monroe Reservoir are number of Hybrid striped bass stocked hectare^{-1}; moronid stocking at Patoka Reservoir and Patoka Reservoir are number of Striped bass stocked hectare^{-1}; warming and discharge at Monroe Reservoir, Patoka Reservoir, Brookville Reservoir, and Cagle's Mill Reservoir are the average change in water temperature at 1.5 m per day during spring/summer and maximum daily discharge recorded during the spring/summer; warming and discharge at Prairie Creek Reservoir and Summit Lake are the average change in air temperature per day during spring/summer and maximum daily rain fall recorded during the spring/summer

Reservoir	Warming, Δ°C day^{-1}	Discharge	Walleye stocking, N hectare^{-1}	Walleye stocking events	Moronid stocking, N hectare^{-1}	Walleye age-0 CPUE
Monroe Reservoir	0.17 (0.024)	58.6 (3.6)*	99 (7.1)	12 (1.2)	18 (4.1)	145 (55.9)
Brookville Reservoir	0.22 (0.020)	75.9 (13.7)*	5,458 (267.2)	7 (0.4)	25 (4.9)	18 (3.8)
Patoka Reservoir	0.14 (0.020)	34.0 (20.6)*	1,212 (306.4)	4 (1.5)	16 (5.6)	9 (2.9)
Cagle's Mill Reservoir	0.22 (0.019)	39.2 (2.6)*	5,293 (665.4)	3 (0.3)	NA	40 (12.8)
Prairie Creek Reservoir	0.16 (0.026)	45.7 (6.35)**	116 (4.9)	3 (0.3)	NA	42 (8.0)
Summit Lake	0.13 (0.029)	59.4 (9.91)**	63 (1.7)	4 (0.7)	NA	3 (1.2)

* indicates discharge is based on dam overflow in m^3 s^{-1}

** indicates discharge is based on total daily rainfall in mm day^{-1}

Table 4. Model selection results; Δpdev = the change in the penalized deviance. Only the top 10 models are shown.

Model	Stocking events	Moronid stocking abundance	Discharge	Warming rate	Δpdev
1	+	+	+		0
2	+		+		78
3		+			81
4	+	+	+	+	171
5	+		+	+	276
6	+	+		+	289
7	+	+			355
8	+			+	411
9		+		+	457
10		+	+		486

Table 5. Posterior distribution mean (standard deviation) of parameters used in the yield-per-recruit model for Walleye and hybrid striped bass.

Parameter	Walleye	Hybrid striped bass	Model
L_∞	716.6 (43.05)	660.1 (20.07)	1
κ	0.245 (0.032)	0.410 (0.045)	1
t_0	-1.43 (0.221)	-0.62 (0.157)	1
Z	-0.84 (0.157)	-0.45 (0.088)	8
α	$4.08*10^{-6}$ ($8.39*10^{-7}$)	$1.00*10^{-5}$ ($1.73*10^{-6}$)	17
β	3.14 (0.032)	3.04 (0.028)	17
Max age	10	13	NA

Table 6. Mean (standard deviation) of estimated natural mortality (M) for Walleye and hybrid striped bass calculated during the yield-per-recruit model simulation.

Model	Walleye	Hybrid striped bass
11 - Quinn and Deriso (1999)	0.46	0.35
12 - Hoenig (1983)	0.42	0.32
13 - Jensen (1996)	0.37 (0.049)	0.62 (0.067)
14 - Peterson and Wroblewski (1984)	0.25 (0.022)	0.25 (0.017)
15 - Chen and Watanabe (1989)	0.46 (0.032)	0.61 (0.044)

Appendix A-1. JAGS code for fitting catch curve models in Chapter 2.

```
model {
#likelihood
for (i in 1:N) {  #loop over observations
num[i]~dpois(mu[i])
log(mu[i])<-alpha[ycn[i]] + z[ycn[i]]*age[i]
}

#priors
for (w in 1:x){
alpha[w]~dnorm(mu.a,tau)
surv[w]~dbeta(a,b)
mort[w]<-1-surv[w]
z[w]<-log(surv[w])
}

mu.a~dnorm(0,0.0001)
sigma~dunif(0,10)
tau<-pow(sigma,-2)
a ~ dgamma(1, 0.01)
b ~ dgamma(1, 0.01)
meansurv<-a/(a+b)
meanmort<-1-meansurv
varsurv<-(meansurv*(1-meansurv))/(a+b+1)
varz<-log(varsurv)
meanz<-log(meansurv)
}
```

Appendix A-2. JAGS code for fitting von Bertalanffy growth models in Chapter 2.

```
model {
  for (i in 1:N) {
    TL[i] ~ dnorm(eta[i], mu.prec)
   eta[i] <- Linf[yrnum[i]] * (1-exp(-k[yrnum[i]] * (Age[i] - t0[yrnum[i]])))
  }

  # Prior for the error precision
  mu.prec <- pow(sigma.y,-2 )
  sigma.y ~ dunif(0,100)

  for (j in 1:yearN){

    Linf[j] <- exp(Linf.1[j])
    k[j] <- exp(k.1[j])
    t0[j] <- exp(t0.1[j]) - 10

    Linf.1[j] ~ dnorm(mu.linf,linf.prec)
    k.1[j] ~ dnorm(mu.k,k.prec)
    t0.1[j] ~ dnorm(mu.t0,t0.prec)
  }


mu.linf ~ dunif(0,10)  #dnorm(0,0.0001)
mu.k ~ dnorm(0,0.0001)
mu.t0 ~ dunif(-3,3)  #dnorm(0,0.0001)

mean.linf<-exp(mu.linf)
mean.k<-exp(mu.k)
mean.t0<-exp(mu.t0) - 10

linf.prec ~ dgamma(0.001, 0.001)
k.prec ~ dgamma(0.001, 0.001)
t0.prec ~ dgamma(0.001, 0.001)

}
```

Appendix A-3. JAGS code for fitting weight-length models in Chapter 2.

```
model {
for (i in 1:N) {
TW[i] ~ dnorm(eta[i], mu.prec)
eta[i] <- alpha * TL[i]^(beta)
}

# Prior for the error precision (=1/Sigma^2)
mu.prec ~ dgamma(0.001, 0.001)
sigma2 <- 1 /mu.prec

beta~ dnorm(0,0.001)
alpha ~ dnorm(0,0.001)

}
```

Appendix A-4. R function for calculating the Beverton-Holt yield-per-recruit models in Chapter 2.

```
ypr<-
function(numitt=1000,S=NULL,umin=0.05,umax=0.6,uinc=0.05,minlength,initialN=100,cm=NULL,linfvec,kvec,t0vec,LWalpha,LWbeta,Mage,Zvec){
  if (missing(minlength))
    stop("Need to specify minimum length.")
  if (missing(linfvec))
    stop("Need to specify Linf mean and standard deviation.")
  if (missing(kvec))
    stop("Need to specify K mean and standard deviation.")
  if (missing(t0vec))
    stop("Need to specify t0 mean and standard deviation.")
  if (missing(LWalpha))
    stop("Need to specify Length-weight intercept mean and standard deviation.")
  if (missing(LWbeta))
    stop("Need to specify Length-weight slope mean and standard deviation.")
  if (missing(Mage))
    stop("Need to specify a maximum age.")
  if (missing(Zvec))
    stop("Need to specify Z mean and standard deviation.")

  uvec<-seq(from=umin,to=umax,by=uinc)

  yieldall<-matrix(1:numitt,nrow=numitt,ncol=1)
  Nharvall<-matrix(1:numitt,nrow=numitt,ncol=1)
  Ndieall<-matrix(1:numitt,nrow=numitt,ncol=1)
  wtall<-matrix(1:numitt,nrow=numitt,ncol=1)
  avglall<-matrix(1:numitt,nrow=numitt,ncol=1)
  linf_dist<-matrix(1:numitt,nrow=numitt,ncol=1)
  K_dist<-matrix(1:numitt,nrow=numitt,ncol=1)
  t0_dist<-matrix(1:numitt,nrow=numitt,ncol=1)
  M_dist<-matrix(1:numitt,nrow=numitt,ncol=1)
  cm_dist<-matrix(1:numitt,nrow=numitt,ncol=1)

  Mall_matrix<-array(dim=c(numitt,5,length(uvec)))  #blank array with numitt rows, 5 cols, and umax*20 blocks

  for (j in 1:(length(uvec))){
    yield<-c()
    NharvOut<-c()
    NdieOut<-c()
    wtOut<-c()
    avglOut<-c()
    linfOut<-c()
    KOut<-c()
```

```
t0Out<-c()
MOut<-c()
MallOut<-c()
cmOut<-c()
maxmorall<-c()
minmorall<-c()


for (k in 1:numitt){
  #time of initial age used for estimates of natural mortality
  ti <- 1

  #time for fish to recruit to a minimum length limit
  TL <- minlength  #Minimum length limit
  linf <- rnorm(1, mean = linfvec[1], sd = linfvec[2])

  #Brody growth coefficient from LVB
  K <- rnorm(1, mean = kvec[1], sd = kvec[2])

  #maximum theoretical weight derived from L-inf and weight to length regression
  tlalpha <- rnorm(1, mean = LWalpha[1], sd = LWalpha[2])
  tlbeta <- rnorm(1, mean = LWbeta[1], sd = LWbeta[2])
  Winf <-  tlalpha * linf^tlbeta

  #Value for incomplete beta functions and other calculations
  t0 <- rnorm(1, mean = t0vec[1], sd = t0vec[2])

  maxage <- Mage  #maximum age for monroe walleye

  #slope of the weight-length relation + 1
  #distribution comes from LW Bayes model
  Q <- tlbeta + 1


  #Instantaneous Rate of total mortality
  Z <- rnorm(1, mean = Zvec[1], sd = Zvec[2])
  S <- exp(Z)

  if(is.null(cm)){
    #M <- 0.30
    hoenig <- exp(1.46 - 1.01 * log(maxage))
    jensen <- 1.50 * K
    perterson_W <- 1.92 * (Winf^-0.25)  #converts pounds to grams
    quinnderiso <- -log(0.01)/maxage
    chenwatanabe <- (1/(maxage-ti)) *
      log(exp(K*maxage)-exp(K*t0))/(exp(K*ti)-exp(K*t0))
```

```
  maxmor<-max(c(hoenig,jensen,perterson_W,quinnderiso,chenwatanabe))
  minmor<-min(c(hoenig,jensen,perterson_W,quinnderiso,chenwatanabe))

  calcmor<-matrix(c(hoenig,jensen,perterson_W,quinnderiso,chenwatanabe),nrow=1,ncol=5)

  M<-runif(1,max=maxmor,min=minmor)
  #M <- (hoenig+jensen+perterson_W+quinnderiso+chenwatanabe)/5
  maxmorall<-c(maxmorall,maxmor)
  minmorall<-c(minmorall,minmor)
  cm_calc<-1-exp(-M)
 }
 else{
  M<- -1 * log((cm-1)*-1)
  maxmorall<-c(maxmorall,M)
  minmorall<-c(minmorall,M)
  cm_calc<-cm
  calcmor<-matrix(rep(M,5),nrow=1,ncol=5)
 }
 u <- uvec[j]

 #Instantaneous Rate of fishing mortality
 Fmort <- (u*-Z)/(1-S)

 #Number of recruits entering the population
 N0 <- initialN

 #time in years to recruit to the fishery (tr - to)
if(TL<linf){
 tr <- (log(1-TL/linf))/-K + t0
}
else{
 tr <- (log(1-TL/(TL+.1)))/-K + t0
}
 r <- tr - t0

 #Number of recruits entering the fishery at some minimum length at time (t):
 Nt <- N0 * exp(-M * tr)

 #Calculate yield
 Y <- ((Fmort*N0*exp(Fmort*r) * Winf) / K) *
  ((pbeta(exp(-K*r),((Fmort+M)/K),Q) * beta(((Fmort+M)/K),Q)) -
    (pbeta(exp(-K*(maxage-t0)),((Fmort+M)/K),Q) * beta(((Fmort+M)/K),Q)))

 #numberof fish harvested
 Nharv<-(Nt*Fmort)/-Z
```

```
    Ndie<-(Nt*M)/-Z
    wt <- Y/Nharv

    avgl<- (wt/tlalpha)^(1/tlbeta)

    yres<-data.frame(Y)
    Nharvres<-data.frame(Nharv)
    Ndieres<-data.frame(Ndie)
    wtres<-data.frame(wt)
    avglres<-data.frame(avgl)
    linfres<-data.frame(linf)
    Kres<-data.frame(K)
    t0res<-data.frame(t0)
    Mres<-data.frame(M)
    cmres<-data.frame(cm_calc)
    yield <- rbind(yield, yres)
    NharvOut<-rbind(NharvOut,Nharvres)
    NdieOut<-rbind(NdieOut,Ndieres)
    wtOut<-rbind(wtOut,wtres)
    avglOut<-rbind(avglOut,avglres)
    linfOut<-rbind(linfOut,linfres)
    KOut<-rbind(KOut,Kres)
    t0Out<-rbind(t0Out,t0res)
    MOut<-rbind(MOut,Mres)
    cmOut<-rbind(cmOut,cmres)
    MallOut<-rbind(MallOut,calcmor)
  }
  yieldall<-cbind(yieldall,yield)
  Nharvall<-cbind(Nharvall,NharvOut)
  Ndieall<-cbind(Ndieall,NdieOut)
  wtall<-cbind(wtall,wtOut)
  avglall<-cbind(avglall,avglOut)
  linf_dist<-cbind(linf_dist,linfOut)
  K_dist<-cbind(K_dist,KOut)
  t0_dist<-cbind(t0_dist,t0Out)
  M_dist<-cbind(M_dist,MOut)
  cm_dist<-cbind(cm_dist,cmOut)
  Mall_matrix[,,j]<-MallOut

}
```

Appendix B-1. JAGS code for multinomial model without covariates, Chapter 3.

```
model {

# Priors
mu.a ~ dnorm(0,0.0001)I(-10,10)
var.a ~ dgamma( 0.001, 0.001 )
sigma.a  <- 1/var.a

for (l in 1:speciesN){
a[l]~dnorm(mu.a,var.a)
  for (k in 1:siteN){
    beta0[l,k] ~ dunif(0,100)  #Abundance
  }
}

#Likelihood
for (i in 1:obs){

logit(p[sp[i],site[i]])<-a[sp[i]]

mu[sp[i],site[i],1]<- p[sp[i],site[i]]
mu[sp[i],site[i],2]<- p[sp[i],site[i]]*(1-p[sp[i],site[i]])
mu[sp[i],site[i],3]<- p[sp[i],site[i]]*(1-p[sp[i],site[i]])*(1-p[sp[i],site[i]])

mu_1[sp[i],site[i]]<-mu[sp[i],site[i],1]
mu_2[sp[i],site[i]]<-mu[sp[i],site[i],2]
mu_3[sp[i],site[i]]<-mu[sp[i],site[i],3]

pi0[sp[i],site[i]]<- 1 - mu[sp[i],site[i],1]-mu[sp[i],site[i],2]-mu[sp[i],site[i],3]
pcap[sp[i],site[i]]<-1-pi0[sp[i],site[i]]

for(j in 1:3){
muc[sp[i],site[i],j]<-mu[sp[i],site[i],j]/(pcap[sp[i],site[i]]+0.0000001) #add a small offset to
prevent division by 0
}

#observed counts model
ncap[sp[i],site[i]]~dbin(pcap[sp[i],site[i]],N[sp[i],site[i]])

#Abundance model
N[sp[i],site[i]] ~ dpois(lambda[sp[i],site[i]])
log(lambda[sp[i],site[i]])<- beta0[sp[i],site[i]]

y[sp[i],site[i],1:3]~dmulti(muc[sp[i],site[i],1:3],ncap[sp[i],site[i]])

}}
```

Appendix B-2. JAGS code for beta-multinomial model without covariates, Chapter 3.

```
model {

# Priors
mu.a ~ dnorm(0,0.0001)I(-10,10)
var.a ~ dgamma( 0.001, 0.001 )
sigma.a  <- 1/var.a

for (l in 1:speciesN){
a[l]~dnorm(mu.a,var.a)
#a[l]~dnorm(0,0.01)I(-10,10)
  for (k in 1:siteN){
    beta0[l,k] ~ dunif(0,100)
  }
}

#Likelihood
for (i in 1:obs){

beta[sp[i],site[i]]~dnorm(0,0.001)I(-10,10)
  p[sp[i],site[i]]~dbeta(alpha.p[sp[i],site[i]],beta.p[sp[i],site[i]])T(0.0001,0.9999)  #capture
probability p follows a beta distribution

alpha.p[sp[i],site[i]]<-mu_p[sp[i],site[i]]*kappa[sp[i],site[i]]

beta.p[sp[i],site[i]]<-kappa[sp[i],site[i]]-mu_p[sp[i],site[i]]*kappa[sp[i],site[i]]

    logit(mu_p[sp[i],site[i]])<-a[sp[i]]  #Covariates of detection can be modeled here

    kappa[sp[i],site[i]]<-exp(beta[sp[i],site[i]])

mu[sp[i],site[i],1]<- p[sp[i],site[i]]
mu[sp[i],site[i],2]<- p[sp[i],site[i]]*(1-p[sp[i],site[i]])
mu[sp[i],site[i],3]<- p[sp[i],site[i]]*(1-p[sp[i],site[i]])*(1-p[sp[i],site[i]])

pi0[sp[i],site[i]]<- 1 - mu[sp[i],site[i],1]-mu[sp[i],site[i],2]-mu[sp[i],site[i],3]
pcap[sp[i],site[i]]<-1-pi0[sp[i],site[i]]

for(j in 1:3){
muc[sp[i],site[i],j]<-mu[sp[i],site[i],j]/pcap[sp[i],site[i]]
      }

#observed counts model
    ncap[sp[i],site[i]]~dbin(pcap[sp[i],site[i]],N[sp[i],site[i]])
```

```
#Abundance model
N[sp[i],site[i]] ~ dpois(lambda[sp[i],site[i]])
log(lambda[sp[i],site[i]])<- beta0[sp[i],site[i]]  #Covariates of abundance can be modeled here

   y[sp[i],site[i],1:3]~dmulti(muc[sp[i],site[i],1:3],ncap[sp[i],site[i]])

}

}
```

Appendix B-3. R code for generating simulated data where capture probability follows a beta distribution, Chapter 3.

```
# Simulate independent data
library(VGAM)
library(reshape)

set.seed(25)

spnum <- 3

nSites <- 10

lambda<-matrix(round(rlnorm((spnum*nSites),2.5,1)),nrow=spnum,ncol=nSites,byrow=T)

shape1<-runif(1,min=0,max=4)
shape2<-runif(1,min=0,max=4)

spdata.1<-c()
trueN<-c()
trueDetect<-c()
N <-c()
p1.1 <- rbeta(nSites,shape1,shape2)
p1.2 <- rbeta(nSites,shape1,shape2)
p1.3 <- rbeta(nSites,shape1,shape2)

p1<-rbind(p1.1,p1.2,p1.3)

for (j in 1:spnum){

#rho
1/(1+shape1+shape2)
#mu
shape1/(shape1+shape2)

#Generate and combine capture probabilities for each pass
  cp<-c()

  for (i in 1:nSites){

    cp<-rbind(cp,(c(p1[j,i], p1[j,i]*(1-p1[j,i]), p1[j,i]*(1-p1[j,i])^2)))

  }
  cp<-matrix(cp,nrow=nSites,ncol =spnum )

  cptemp<-data.frame(cp,species=j)
  trueDetect<-rbind(trueDetect,cptemp)
```

```
  #calculate pi at 0 and pcap
  pi0<-1-rowSums(cp)
  pcap<-1-pi0

  for (k in 1:nSites){
    N[k] <- rpois(1, lambda[j,k]) #True abundance at each site
  }

  Ntemp<-data.frame(N,species=j)
  trueN<-rbind(trueN,Ntemp)

  ncap<-c()

  #Generate number collected at each site based on overall capture probability
  for (i in 1:nSites){
    ncap[i]<-rbinom(1,N[i],pcap[i])
  }

  y <- matrix(NA, nSites, 3)

  #Generate multinomial cell probabilties for capture history
  for(i in 1:nSites) {
    y[i,] <- rmultinom(1, ncap[i], cp[i,])
  }

  spdat<-melt(y)

  names(spdat)[1]<-"siteN"
  names(spdat)[2]<-"pass"

  spdat<-data.frame(spdat,spnum=j)

  spdata.1<-rbind(spdata.1,spdat)  #Data used
}

spdata_all<-data.frame(spdata.1)
spdata<-subset(spdata_all,spdata_all$pass==1)

y_1<-cast(spdata_all,formula=spnum~siteN~pass,sum,value="number",fill=NA)

ncap<-as.matrix(cast(spdata_all,formula=spnum~siteN,sum,value="number",fill=NA))
ymax<-ncap
```

Appendix C-1. List of species encountered and total number sampled.

Family	Common name	Scientific name	N
Catostomidae	Black Redhorse	*Moxostoma duquesnii*	30
Catostomidae	Golden Redhorse	*Moxostoma erythrurum*	227
Catostomidae	Northern Hogsucker	*Hypentelium nigricans*	337
Catostomidae	Quillback Carpsucker	*Carpiodes cyprinus*	5
Catostomidae	River Redhorse	*Moxostoma carinatum*	1
Catostomidae	Shorthead Redhorse	*Moxostoma macrolepidotum*	3
Catostomidae	Silver Redhorse	*Moxostoma anisurum*	2
Catostomidae	Spotted Sucker	*Minytrema melanops*	3
Catostomidae	White Sucker	*Catostomus commersonii*	301
Centrarchidae	Black Crappie	*Pomoxis nigromaculatus*	3
Centrarchidae	Bluegill	*Lepomis macrochirus*	465
Centrarchidae	Green Sunfish	*Lepomis cyanellus*	1013
Centrarchidae	Hybrid Sunfish		16
Centrarchidae	Largemouth Bass	*Micropterus salmoides*	72
Centrarchidae	Longear Sunfish	*Lepomis megalotis*	2054
Centrarchidae	Orangespotted Sunfish	*Lepomis humilis*	1
Centrarchidae	Pumpkinseed Sunfish	*Lepomis gibbosus*	21
Centrarchidae	Redear Sunfish	*Lepomis microlophus*	16
Centrarchidae	Rock Bass	*Ambloplites rupestris*	247
Centrarchidae	Smallmouth Bass	*Micropterus dolomieu*	71
Centrarchidae	White Crappie	*Pomoxis annularis*	1
Clupeidae	Gizzard Shad	*Dorosoma cepedianum*	11
Cottidae	Mottled Sculpin	*Cottus bairdii*	159
Cyprinidae	Bigeye Chub	*Hybopsis amblops*	7
Cyprinidae	Bigeye Shiner	*Notropis boops*	1
Cyprinidae	Blacknose Dace	*Rhinichthys atratulus*	23
Cyprinidae	Bluntnose Minnow	*Pimephales notatus*	1711
Cyprinidae	Central Stoneroller	*Campostoma anomalum*	830
Cyprinidae	Common Carp	*Cyprinis carpio*	56
Cyprinidae	Creek Chub	*Semotilus atromaculatus*	676
Cyprinidae	Emerald Shiner	*Notropis atherinoides*	37
Cyprinidae	Fathead Minnow	*Pimephales promelas*	3
Cyprinidae	Hornyhead Chub	*Nocomis biguttatus*	5
Cyprinidae	Mimic Shiner	*Notropis volucellus*	213
Cyprinidae	Mississippi Silvery Minnow	*Hybognathus nuchalis*	10
Cyprinidae	Redfin Shiner	*Lythrurus umbratilis*	62
Cyprinidae	River Chub	*Nocomis micropogon*	34
Cyprinidae	Sand Shiner	*Notropis stramineus*	496
Cyprinidae	Silver Shiner	*Notropis photogenis*	8
Cyprinidae	Silverjaw Minnow	*Ericymba buccata*	347

Cyprinidae	Spotfin Shiner	*Cyprinella spiloptera*	535
Cyprinidae	Steelcolor Shiner	*Cyprinella whipplei*	86
Cyprinidae	Striped Shiner	*Luxilus chrysocephalus*	224
Cyprinidae	Suckermouth Minnow	*Phenacobius mirabilis*	20
Esocidae	Redfin Pickerel	*Esox americanus americanus*	10
Fundulidae	Blackstripe Topminnow	*Fundulus notatus*	41
Ictaluridae	Brindled Madtom	*Noturus miurus*	3
Ictaluridae	Channel Catfish	*Ictalurus punctatus*	32
Ictaluridae	Flathead Catfish	*Pylodictis olivaris*	7
Ictaluridae	Tadpole Madtom	*Noturus gyrinus*	13
Ictaluridae	Yellow Bullhead	*Ameiurus natalis*	112
Percidae	Banded Darter	*Etheostoma zonale*	42
Percidae	Blackside Darter	*Percina maculata*	18
Percidae	Fantail Darter	*Etheostoma flabellare*	26
Percidae	Greenside Darter	*Etheostoma blennioides*	332
Percidae	Johnny Darter	*Etheostoma nigrum*	200
Percidae	Logperch	*Percina caprodes*	188
Percidae	Orangethroat Darter	*Etheostoma spectabile*	283
Percidae	Rainbow Darter	*Etheostoma caeruleum*	235
Percidae	Slenderhead Darter	*Percina phoxocephala*	1
Percidae	Walleye	*Sander vitreus*	1
Petromyzontidae	Lamprey ammocoetes	*Petromyzontidae sp.*	10
Poeciliidae	Western Mosquitofish	*Gambusia affinis*	6
Salmonidae	Rainbow Trout	*Gambusia affinis*	1
Sciaenidae	Freshwater Drum	*Aplodinotus grunniens*	1

Appendix D-1. Posterior distribution of species specific capture probabilities from the multinomial and beta-multinomial models without covariates of capture probability. 2.5% and 97.5% represents the 95% Credible Intervals and 50% represents the median of the posterior distribution.

		Multinomial model			Beta-Multinomial model		
Family	Species	2.50%	50%	97.50%	2.50%	50%	97.50%
Catostomidae	Black Redhorse	0.19	0.37	0.47	0.21	0.43	0.56
Catostomidae	Golden Redhorse	0.29	0.37	0.44	0.29	0.43	0.53
Catostomidae	Northern Hogsucker	0.31	0.38	0.45	0.32	0.44	0.54
Catostomidae	Quillback Carpsucker	0.10	0.36	0.48	0.16	0.43	0.59
Catostomidae	River Redhorse	0.18	0.37	0.54	0.20	0.43	0.62
Catostomidae	Shorthead Redhorse	0.24	0.37	0.67	0.23	0.44	0.65
Catostomidae	Silver Redhorse	0.17	0.37	0.54	0.20	0.43	0.62
Catostomidae	Spotted Sucker	0.14	0.37	0.49	0.18	0.43	0.59
Catostomidae	White Sucker	0.28	0.36	0.43	0.32	0.44	0.55
Centrarchidae	Black Crappie	< 0.01	0.12	0.52	0.02	0.33	0.54
Centrarchidae	Bluegill	0.23	0.31	0.39	0.25	0.37	0.46
Centrarchidae	Green Sunfish	0.13	0.19	0.25	0.13	0.32	0.41
Centrarchidae	Hybrid Sunfish	< 0.01	0.15	0.52	0.02	0.33	0.51
Centrarchidae	Largemouth Bass	< 0.01	0.09	0.28	0.01	0.29	0.43
Centrarchidae	Longear Sunfish	0.26	0.30	0.34	0.30	0.41	0.49
Centrarchidae	Orangespotted Sunfish	< 0.01	0.11	0.51	0.02	0.33	0.55
Centrarchidae	Pumpkinseed Sunfish	0.32	0.74	0.91	0.06	0.36	0.80
Centrarchidae	Redear Sunfish	< 0.01	0.12	0.46	0.02	0.33	0.49
Centrarchidae	Rock Bass	0.26	0.37	0.47	0.25	0.37	0.47
Centrarchidae	Smallmouth Bass	< 0.01	0.11	0.32	0.02	0.31	0.45
Centrarchidae	White Crappie	< 0.01	0.13	0.64	0.02	0.33	0.56
Clupeidae	Gizzard Shad	< 0.01	0.01	0.52	< 0.01	< 0.01	1.00
Cottidae	Mottled Sculpin	0.18	0.33	0.46	< 0.01	< 0.01	0.49
Cyprinidae	Bigeye Chub	0.20	0.37	0.59	0.26	0.39	0.51
Cyprinidae	Bigeye Shiner	0.17	0.34	0.55	0.27	0.39	0.51
Cyprinidae	Blacknose Dace	0.25	0.40	0.61	0.30	0.40	0.54
Cyprinidae	Bluntnose Minnow	0.20	0.25	0.29	0.24	0.38	0.45
Cyprinidae	Central Stoneroller	0.38	0.43	0.48	0.33	0.41	0.57
Cyprinidae	Common Carp	0.20	0.34	0.49	0.28	0.39	0.49
Cyprinidae	Creek Chub	0.26	0.32	0.38	0.33	0.40	0.47
Cyprinidae	Emerald Shiner	0.16	0.31	0.45	0.26	0.39	0.50
Cyprinidae	Fathead Minnow	0.20	0.37	0.60	0.28	0.40	0.52
Cyprinidae	Hornyhead Chub	0.14	0.31	0.46	0.25	0.39	0.49
Cyprinidae	Mimic Shiner	0.28	0.38	0.47	0.30	0.40	0.48
Cyprinidae	Mississippi Silvery Minnow	0.20	0.36	0.56	0.28	0.40	0.52
Cyprinidae	Redfin Shiner	0.16	0.30	0.42	0.25	0.39	0.48

Cyprinidae	River Chub	0.14	0.29	0.41	0.24	0.39	0.47
Cyprinidae	Sand Shiner	0.24	0.32	0.38	0.28	0.38	0.45
Cyprinidae	Silver Shiner	0.18	0.34	0.53	0.27	0.39	0.50
Cyprinidae	Silverjaw Minnow	0.30	0.37	0.45	0.31	0.40	0.47
Cyprinidae	Spotfin Shiner	0.33	0.40	0.46	0.32	0.40	0.47
Cyprinidae	Steelcolor Shiner	0.28	0.41	0.54	0.31	0.40	0.51
Cyprinidae	Striped Shiner	0.30	0.39	0.49	0.32	0.40	0.50
Cyprinidae	Suckermouth Minnow	0.16	0.32	0.46	0.25	0.39	0.48
Esocidae	Redfin Pickerel	< 0.01	0.08	0.73	< 0.01	< 0.01	1.00
Fundulidae	Blackstripe Topminnow	< 0.01	0.04	0.42	< 0.01	< 0.01	0.38
Ictaluridae	Brindled Madtom	< 0.01	< 0.01	0.11	< 0.01	< 0.01	0.13
Ictaluridae	Channel Catfish	< 0.01	< 0.01	0.14	< 0.01	< 0.01	0.11
Ictaluridae	Flathead Catfish	< 0.01	< 0.01	0.12	< 0.01	< 0.01	0.20
Ictaluridae	Tadpole Madtom	< 0.01	< 0.01	0.09	< 0.01	< 0.01	0.08
Ictaluridae	Yellow Bullhead	< 0.01	< 0.01	0.09	< 0.01	< 0.01	0.08
Percidae	Banded Darter	0.04	0.20	0.35	0.03	0.20	0.35
Percidae	Blackside Darter	0.02	0.18	0.34	0.02	0.19	0.34
Percidae	Fantail Darter	0.03	0.19	0.35	0.02	0.20	0.35
Percidae	Greenside Darter	0.14	0.22	0.31	0.08	0.21	0.35
Percidae	Johnny Darter	0.15	0.25	0.39	0.06	0.21	0.39
Percidae	Logperch	0.08	0.20	0.30	0.04	0.20	0.32
Percidae	Orangethroat Darter	0.02	0.15	0.24	0.03	0.18	0.30
Percidae	Rainbow Darter	0.08	0.19	0.28	0.03	0.19	0.32
Percidae	Slenderhead Darter	0.03	0.19	0.43	0.03	0.20	0.39
Percidae	Walleye	0.03	0.19	0.43	0.03	0.20	0.39
Petromyzontidae	Lamprey ammocoetes	< 0.01	< 0.01	0.28	< 0.01	< 0.01	0.99
Poeciliidae	Western Mosquitofish	< 0.01	< 0.01	0.20	< 0.01	< 0.01	0.99
Salmonidae	Rainbow Trout	< 0.01	< 0.01	0.42	< 0.01	< 0.01	0.99
Sciaenidae	Freshwater Drum	< 0.01	< 0.01	0.77	< 0.01	< 0.01	0.99